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STUDIES IN AUSTRALIAN ESTUARINE HYDROLOGY

I. INTRODUCTORY AND COMPARATIVE FEATURES

By D. J. Rochford*

(*Manuscript received November* 21, 1950)

Summary

In this paper is presented an introduction to the methods involved in the collection, analysis, and interpretation of Australian estuarine hydrological data collected by the Division of Fisheries, C.S.I.R.O. The chief features of the circulation and mixing exchanges in such systems have been discussed.

A review of the zonal distribution of the principal hydrological properties of estuarine waters, and of certain selected chemical properties of the bottom deposits, has led to the establishment of a schematic zonal diagram by which the hydrological classification of estuarine systems can be attempted.

An examination of the zonal composition of certain estuarine systems has been attempted, and on the basis of such composition and the volume of water, a theory of zonal dominance has been developed. The development of conflicts of hydrological properties, by reason of tidal rise and fall of water level, has been examined, and some idea of the range of this derived property demonstrated by an examination of the diurnal range of chlorinity in certain estuarine systems.

Some general aspects of the productivity of estuarine waters and bottom deposits have been examined and a number of hypotheses concerning the role of phosphates in their respective productivity levels have been postulated.

An examination of the chemical interaction between the water and its associated bottom deposit has been made. The relation of these studies to oyster cultivation and methods of mud flat enrichment for promotion of oyster growth has been discussed.

I. INTRODUCTION

Although long-term studies on the productivity and ecological aspects of the neritic waters in certain parts of the world, e.g., the Channel investigations of the Plymouth Marine Laboratory, have been carried out for some considerable time, no parallel investigations of the hydrological features of estuarine waters have been conducted. It is true that ecological and hydrological investigations of specialized regions of the estuarine environment have been carried out (Evans 1947; Fraser 1932; Marshall and Orr 1927; Milne 1937; Moore 1930, 1931; Stephens 1929) but no extensive or persistent hydrological and biological work, such as might yield information on the productivity and zonal characteristics of an estuary considered as a mixing region for neritic and freshwater components, has been attempted. The work of Alexander, Southgate, and Bassindale (1935) on the Tees estuary, although dictated by the needs of an *ad hoc* pollution problem, represents a considerable advance on hydrological papers dealing with smaller regions of the estuarine system.

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The longitudinal variation in chlorinity conditions in an estuarine system and some indication of hydrological zonation can be ascertained from the above paper. The diurnal rhythm of chlorinity at various points within the system was also measured. However, as the work was not repeated in sufficient detail over a period of years, no indication of the seasonal change in such hydrological conditions could be gained. The question of productivity in the Tees estuarine system was not considered. A more recent paper by Bassindale (1943) considers in further detail the dynamics of salinity variations in the Tees and Severn estuaries of Great Britain, but again does not consider the productivity of these estuaries.

In the U.S.A., a paper by Nash (1947) gives the hydrological properties of the Patuxent River draining into Chesapeake Bay. This work was repeated over a period of years so that averages and seasonal range of hydrological properties can be computed. The sampling, however, was not extended into the adjoining neritic or fluviatile waters, nor was any attempt made to estimate productivity.

In Chesapeake Bay itself the hydrological properties of this semi-estuarine body of water have been investigated by Newcombe and Lang (1939) and by Newcombe and Brust (1940), but no long-term sampling upon which seasonal cycles might be based was attempted.

In France, the work of Varlet and Menaché (1947) on the Moros estuary in Concarneau has been guided by the results of the Tees estuary survey. The seasonal range of hydrological properties for this estuary, together with consideration of mixing phenomena, was discussed by these authors.

The mixing of neritic and fluviatile waters in an estuarine basin has been discussed in detail by Tully (1949), but his results cannot be considered representative of mixing exchanges in all estuarine systems, and, as will be shown in this paper, do not agree with the processes of mixing exchanges in most Australian estuarine systems (Section IV).

The studies by the University of Quebec on the hydrology of the St. Lawrence estuary, e.g., Vachon, Gaudry, and Bernard (1938), Gaudry (1938), and Nadeau (1938) are probably the most systematic and detailed available work on the estuarine environment. However, the great depths of water in this estuary render this estuarine environment almost neritic, if not oceanic, in most of its characteristics, with tidal influence greatly diminished in most parts of the estuarine basin. The work of Tremblay and Lauzier (1940), in which they are able to demonstrate the existence at subsurface levels in the St. Lawrence estuary of oceanic waters derived at considerable distances from the Labrador Sea and Atlantic Ocean, supports the neritic rather than estuarine classification of these estuarine waters. The lack of fluviatile and brackish water sampling below a salinity of about 20 per mille also limits the establishment of the full zonal features of this system.

In Australia, prior to the work of the Division of Fisheries, C.S.I.R.O., no information on the hydrology of Australian estuarine systems was available. The work of the Sydney University Zoology Department (Dakin, Bennett, and Pope 1948) and of the various State museums on the systematics of the estuarine fauna and flora is a valuable contribution to estuarine biology, but it is for the most part unsuitable for ecological correlation with the broader zonal hydrological characteristics of such systems as are demonstrated in this paper. The work of Miss M. Morris, whose estuarine macro-plankton counts are given in Appendix VIII, demonstrates the possibilities of correlations between hydrological zones and plankton distribution in estuarine systems. This lack of broad biological data in estuarine systems is particularly felt when comparative estimates of productivity between systems are attempted. It represents a fruitful field for the marine ecologist.

TABLE 1

ANNUAL OUTPUT OF OYSTERS, OSTREA COMMERCIALIS, FROM, AND SOME HYDROLOGICAL CHARACTERISTICS OF SELECTED LOCALITIES ALONG THE NEW SOUTH WALES COAST, JULY 1946-JUNE 1947

(Data from annual reports, N.S.W. State Fisheries Department)

Locality	Total No. Bags	Zonal Classification	Average Chlorinity Conflict in Growing Zone
Richmond R.	564	Freshwater	Moderate
Hastings R.	2,047	Freshwater	Moderate
Macleay R.	38	Freshwater	High
Pt. Stephens	15,114	Marine-tidal	Low
Hawkesbury R.	3,729	Gradient	Moderate
George's R.-Botany Bay	8,511	Tidal	Low
Clyde R.	1,684	Gradient	Low

In eastern Australian estuarine systems, shallowness, together with tidal mixing, prevents the formation of any marked stratification, and vertical turbulence is particularly well developed (Section IV). Moreover, except for some systems in northern New South Wales, the overall phosphate level is low, with little run-off contribution. This vertical turbulence and low phosphate level permits little or no phytoplankton productivity (data in possession of Division of Fisheries, C.S.I.R.O.) in most estuarine systems, except in such as are wholly or in part marine-dominated and almost neritic in their hydrological features.

In spite of this absence of phytoplankton production, it is apparent that the productivity level of eastern Australian estuarine systems is reasonably high by comparison with that of the adjoining neritic waters. In New South Wales, for example, the catch of mullet, which obtains most of its food in estuaries (Kesteven 1942), provides a major portion of the New South Wales fish catch. Table 1 gives for a typical year the production of New South Wales oysters, which are entirely dependent upon estuarine nutritive reserves.

As the growth rate of oysters in crowded conditions in the intertidal zone is at the rate of some 4 g. meat weight per year (Humphrey 1941), the growth of these oyster stocks, which at this rate averages 100 tons per annum, represents a considerable intake of food substances.

The estuarine hydrological investigations of this Division in eastern Australian waters were initially part of an oyster research programme, and were designed to explain the differing values of various estuarine systems as environments favouring spatting or fattening phases of oyster cultivation, or both. It was well known in the trade that certain systems, e.g., that of Port Hacking, support a stunted adult population, but that spawning and subsequent larval survival to the fixation stage are good. In other systems, e.g., George's River, although adult growth and fattening are excellent, larval survival and the resultant spatfall are particularly poor.

Primarily, therefore, the hydrological investigations were aimed at the elucidation of such pronounced differences in oyster development in estuarine systems. It was soon realized, however, that to solve even these important local problems, a large and comprehensive comparative study of representative types of Australian estuarine systems should be undertaken. It was also apparent that the study of estuarine productivity *per se* would provide additional vital evidence.

There is an absence of any great phytoplankton production in the greater portion of most estuarine systems. This indicates that estuarine productivity should be found to be controlled by factors that differ in nature and degree of influence from those operative in the open sea (Riley 1946) or fresh water (Pennak 1946).

The work of the European pond culturists, and especially Demoll (1925), has demonstrated the importance of the retention of phosphates in the bottom deposits as a primary factor governing the productivity of the overlying water. In Europe, the work of Breest (1921) has clearly demonstrated that the type of fertilizer added to the pond bottom can control the quality of plankton in the subsequent bloom.

In Indonesia, tambak pond cultivation is dependent upon the development of a suitable bottom deposit. The type of dry fallowing practised upon such deposits largely determines the kind of phytoplankton or algal growth in the subsequent bloom (Schuster 1949).

The more fundamental work by Mortimer (1941, 1942) in his investigations of the exchange of nutrient substances between mud and water in freshwater English lakes, suggested that the chemical and physical characteristics of bottom deposits might play a significant part in estuarine productivity.

In these Australian investigations it was, therefore, proposed to carry out hydrological investigations involving determination of chlorinity, dissolved gases, and the principal inorganic nutrients; to make the determinations at sufficient points within each system to enable longitudinal and zonal features to be established; and to repeat over a sufficient period of time to enable seasonal and long-term effects to be ascertained. To secure comparative results these hydrological studies were to be spread over a number of systems likely to reveal all variations from a standard to be established.

Hydrological sampling was therefore regularly carried out from mouth to source in a number of systems of different type, not only in New South Wales, but in Victoria, Tasmania, Western Australia, and latterly, Queensland. In association with these hydrological investigations an accompanying and comparable bottom sampling programme on a less intensive scale was prosecuted. In the analysis of these bottom samples, prime importance was attached to the phosphatic constituents because of their low level in the waters of most Australian estuarine systems, and to the ferric iron compounds which Mortimer (1941) and Ohle (1937) have shown to be important in controlling the exchange of phosphatic nutrients between mud and water.

The importance of organic humus in controlling anion and cation exchange in soil (Ohle 1937) and its possible similar role in aquatic soils was considered in including carbon and nitrogen analyses in the programme. Use was also made of such constituents as an index of comparative microbiological activity.

Although recent work on soils has shown that some adsorption can occur on the surface of soil particles up to sand size, the bulk of adsorption is associated with the silt and colloidal soil particles. The analysis of bottom deposits was, therefore, confined to particles within the silt-colloidal size group. (See also Section III (*b*) (i).)

In a recently available paper Czensky (1943) suggested that the methods of soil analysis should be used in limnological bottom investigations. He proposed that certain anion and cation exchange characteristics, together with their saturation deficits, should be calculated and used in the estimation of relative fertility. Whilst it has been our practice in these estuarine studies to use, whenever possible, existing or slightly modified soil analytical methods, certain basic differences between the soil and estuarine bottom deposits necessitated caution in the interpretation, according to conventional soil methods, of results obtained by their use. In the first place, the estuarine bottom deposits are always waterlogged by and in intimate connection with their bounding water mass. Secondly, in estuarine bottom deposits the basic level of organic matter is only in part derived from *in situ* biological processes, and in some cases appears to be completely derived from external sources. This situation complicates, for example, the interpretation of carbon and nitrogen levels and of their C/N ratio in such bottom deposits.

To provide evidence on the seasonal spatial and depth variation of such constituents in a marine mud, routine analysis of muds collected at various stations within the intertidal zone at Shell Point, George's River, were conducted. At these stations the vertical distribution and movement of such constituents were especially studied. To ascertain the effect of phosphate levels on the productivity of the intertidal waters, additions of a phosphate enrichment mixture were made to muds and followed by chemical and biological analyses of the mud and intertidal waters.

In south-west Australian estuarine systems, the absence of a persistent tidal mixing permits of the development of vertical stratification to a remarkable degree in view of the extreme shallowness of most of the systems in the area. During the winter runoff into these systems the phosphate content is quite high, but the overall productivity, as judged by subsequent retention and turnover of nutrients within the system, is poor. Phytoplankton production, as shown by the work of Serventy (personal communication) is not high.

The earlier hydrological work on these systems was a continuation of the investigations in the eastern Australian system. It was soon realized, however, that the absence of tide developed certain hydrological and productivity features that were not comparable with those in corresponding eastern Australian systems.

The circulation pattern and the extreme development of stratification isolate the bottom waters and bottom muds from the surface waters to a remarkable degree. In these systems, therefore, special attention was paid to these particular aspects.

This paper is the first in a series on Australian estuarine hydrology. It presents the chief comparative features of Australian estuarine systems, together with the methods of analysis and terminology employed. Though it is necessary to establish certain comparative features of a type system, no detailed consideration is given to the hydrological features of any particular system. In succeeding papers, certain systems capable of classification in a hydrological grouping will be discussed in detail, and any omission of detail in the present paper is to be explained on that account. At an early date, too, it is hoped to present a paper containing results of the long-term study of variations, at surface and sub-surface levels, of the chemical properties of intertidal muds, and of the effect of phosphate enrichment mixtures on such muds. The relationship of these mud properties to estuarine productivity and to oyster growth in particular will then be fully discussed. It is apparent that, in this field of studies, the use of radioactive tracers will prove of great importance, and steps are being taken to include such tracer studies in this programme.

In order to avoid confusion, the difference between an estuarine and a brackish water environment needs to be stressed. Brackish water is generally understood to mean salt water diluted by fresh water or rain water and need not necessarily be influenced by tidal movement. We can thus distinguish brackish water lakes, lagoons, and other dynamically stable environments. By an estuarine environment we mean one that is not only subject to long-term alteration in chlorinity and other properties by seasonal variation in the amount of freshwater or rainfall dilution, but is also subject to a persistent circulation exchange of elements between the estuarine system and the adjoining neritic waters. Tidal rise and fall of water level is a prime factor in the development of these persistent circulation exchanges.

II. GEOGRAPHICAL SOURCES OF DATA (FIG. 1)

The hydrological and bottom data used in the preparation of the papers of this series were gathered (since the dates specified) from the areas set out in Table 2.

TABLE 2

SOURCES OF DATA

Location	Hydrological	Bottom Investigations
New South Wales:		
Port Hacking	October 1940	November 1945
George's River-Botany Bay	October 1940	April 1945
Port Stephens	June 1942	May 1947
Hawkesbury River	January 1946	September 1945
North Coast estuaries	August 1946	August 1946
South Coast estuaries	November 1945	November 1945
Wagonga Inlet	April 1942	November 1945
Shell Point	January 1942	June 1946
Victoria:		
Gippsland Lakes	February 1946	February 1946
Port Phillip	April 1947	—
Tasmania:		
Derwent River	February 1947	January 1946
Huon River	February 1947	February 1947
Tamar River	February 1947	February 1947
D'Entrecasteaux Channel	March 1947	—
Pittwater	March 1949	March 1949
South-West Australia:		
Leschenault Inlet	September 1946	September 1946
Peel Harvey Inlet	September 1946	September 1946
Hardy Inlet	September 1946	September 1946
Nornalup Inlet	September 1946	September 1946
Denmark Inlet	September 1946	September 1946
King George's Sound	September 1946	September 1946

Within each of these estuarine systems, at a location determined by its importance in assessing chlorinity conflict values (Section V (*e*)), continuous hydrological sampling over a full diurnal tidal cycle has been conducted. This normally occurred at hourly intervals to determine tide height and water and air temperatures; while at two-hourly intervals water samples were collected. Complete lists of the hydrological data and chemical analyses of bottom deposits collected during these investigations will be issued as separate publications of C.S.I.R.O., Melbourne, and will be available on request to the Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

III. METHODS

(*a*) *Water Analysis*

(i) *Temperature.*—Temperatures were always taken with a deep-sea mercury reversing thermometer but are probably consistently reliable only to about 0.1°C. In the studies on mud flat temperatures (Section V (*a*) (iv) (4)) a resistance thermometer designed by the Division of Physics, C.S.I.R.O., was utilized. Resistance elements enclosed in monel metal containers were fixed in the mud and water at various locations and depths, and leads taken to terminal posts on a jetty. A bridge unit was coupled to these terminals, and the resistance of the element, transformed into temperature units, was read directly.*

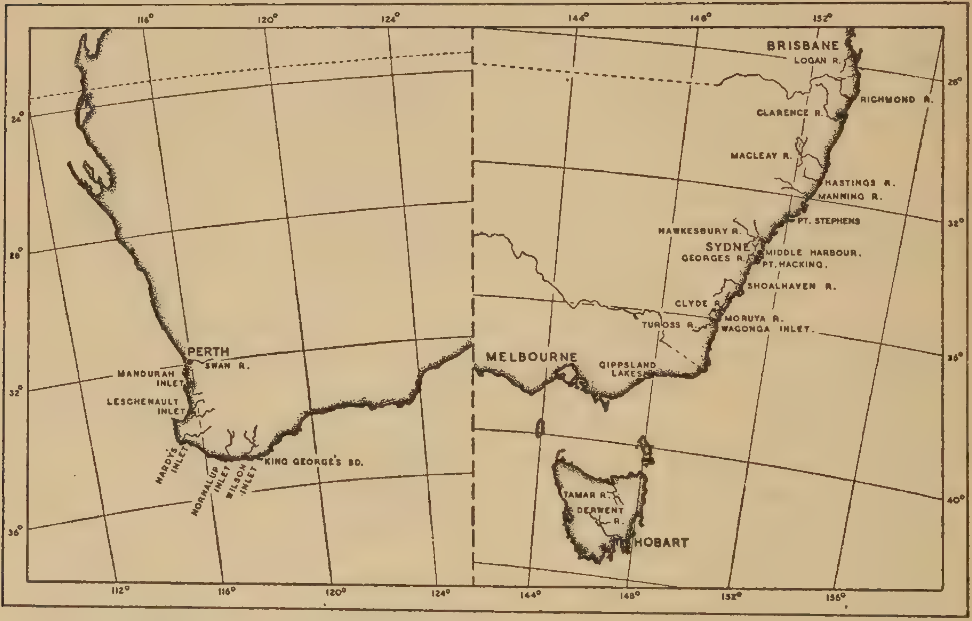

Fig. 1.—Location of the principal estuarine systems referred to in the text.

(ii) *Sampling.*—Water samples at surface and sub-surface depths were taken with a Nansen reversing bottle. Bottom water samples to within a metre of the bottom were taken wherever the depth exceeded 4 metres. At depths less than 4 metres a mid-water sample only was taken. Bottom mud samples were taken with a tube sampler fitted with a piston, the unit being strapped to the end of a pole during use. The upper three inches of mud were sampled with this unit.

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* Although this principle in thermometry is not new, it is interesting to note that the perfection of commercially produced thermistors or thermally sensitive resistances (Becker, Green, and Pearson 1947) has recently developed greater interest in this method of temperature measurement in limnology (Platt and Shoup 1950) and in general experimental biology (Platt and Wolf 1950).

(iii) *Preservation.*—No field determinations were attempted. The unpreserved samples were transported to the laboratory as rapidly as possible for analysis, and a period of days sometimes elapsed before the laboratory analyses could be carried out. A considerable number of tests of the reliability of chloroform, toluene, and sodium fluoride, as preservatives for phosphate, have been carried out and will be published in a subsequent paper. It is sufficient to note at this stage that the use of any of these preservatives does not have any marked effect on the retardation of storage errors. Moreover, in a number of the tests, the phosphate figure for sea-water stored without preservative in the dark for one week was not appreciably different from the original figure. It has been the Divisional practice, therefore, to store all samples for nutrient analyses in the dark, without chemical preservation, immediately after collection and to reduce the time elapsing between collection and analysis to the minimum. For pH determinations, however, 5 drops of saturated mercuric chloride per 30 ml. were used as a preservative, and in addition the sample bottles were occasionally kept under water prior to laboratory analysis in order to prevent CO_2 exchanges with the air. The use of mercuric chloride was first suggested by Ibânez (1930), and its use in marine studies has been confirmed by the author during the hydrological investigations of F.R.V. "Warreen" in eastern Australian waters during 1938-42. Subsequently, however, it has been found that saturated mercuric chloride solution, because of the acidity of the salt itself, lowers the pH of unbuffered samples, such a lowering becoming significant below a chlorinity of about 1°/oo. Any pH samples to which mercuric chloride has been added as a preservative are unreliable below a chlorinity of 1-2 per cent. Only *in situ* field determinations can be considered reliable in the freshwater region of an estuarine system.

(iv) *Chlorinity.*—Chlorinity was determined by the Mohr technique as modified for use in the determination of the chlorinity of sea-water by Oxner and Knudsen (1920) using a Knudsen bulb burette and a 10 ml. tap pipette. Copenhagen and Woods Hole standard sea-water were used as reference standards. The routine precision of this determination was of the order of ± 0.025°/oo Cl.

(v) *Dissolved Oxygen.*—Oxygen was determined by Winkler's classical method recently reviewed by Thompson and Robinson (1939). The first two reagents were added immediately after collection and the acid some time later. A convenient field kit for the carrying and automatic delivery of the oxygen reagents has been devised and a photograph of the unit is given in Plate 1. The pipettes used were modified from a design described in Sverdrup and Soule (1933). The titration of the iodine solution was carried out in the laboratory at a later date. The data are given as ml./l. at 20°C. Oxygen saturation figures were calculated using Fox's Tables (1907). The routine precision of this determination was about ± 0.025 ml. O_2/l.

(vi) *Phosphate Phosphorus.*—Inorganic phosphates were determined by Atkins's (1923) modification of Denigès's (1920) technique, following a procedure given by Robinson and Thompson (1948). It was found necessary to be very accurate in the delivery of the 1 per cent. stannous chloride and a 0.1 ml. addition from a microburette was adopted. It was found convenient to maintain a 40 per cent. stannous chloride in hydrochloric acid stock solution under liquid paraffin, and by dilution, to prepare as required the necessary quantity of the 1 per cent. stannous chloride reducing solution. The 40 per cent. solution was efficiently protected from oxidation by this method of storage. A Seiwell type of colour comparator (1935) with a tube depth of 30 cm. was used up to 1947, but from that date a Spekker photoelectric absorptiometer, using 4 cm. cells and Ilford 608 filters, has been used. The data were entered as μg. phosphate phosphorus per litre, and no salt error corrections have been applied. The routine precision of this determination was about ± 0.5 μg. P/l. in the range 0-10 μg., and ± 1-2 μg. in the range of 10-20 μg. At higher concentrations an average of about ± 10 per cent. error was encountered.

(vii) *Total Phosphorus.*—Following the technique of Robinson (1941), 0.2 ml. 72 per cent. perchloric acid was added to a 100 ml. sample aliquot, which was digested at 150°C. on a sand tray until white fumes appeared. 100 ml. of distilled water and 2 drops of phenolphthalein were then added. If the sample reacted alkaline sufficient perchloric acid was added to discharge the colour, and the digest was allowed to stand 24 hours. At the end of this period the solution was neutralized with 5N ammonium hydroxide, and the phosphate content determined. Fairly frequent blank determinations on 0.2 ml. of the 72 per cent. perchloric acid were made, and the blank error was kept below a significant figure by careful selection of acid. Organic phosphate was calculated as the difference between the total and inorganic phosphate figures.

Kalle (1933) has criticized this method of digestion and suggested the use of fuming sulphuric acid with the addition of a little copper salt. However, it is the author's experience that the use of sulphuric acid gives consistently lower organic phosphate than the original inorganic figure. In his opinion this is probably due to pyrophosphate formation and the subsequent difficulty in converting it into orthophosphate by boiling. Berger (1938) considers that Kalle's method gives low results because of incomplete oxidation.

Robinson's method does not eliminate the interference of arsenates, and all organic phosphate figures will therefore include any arsenates present in the sample. Harvey's recent method (Armstrong and Harvey 1950) for the determination of organic phosphates has not yet been tried by the author.

In turbid samples containing clay colloids some phosphate must be released from inorganic soil phosphates by acid digestion, and will be included in the organic phosphate figure. Allowance has to be made for this error in judging the significance of organic phosphate figures from turbid water areas.

(viii) *Particulate and Soluble Organic Phosphates.*—The organic phosphate figure as determined above may be composed of soluble and particulate organic phosphate elements. By centrifuging a further aliquot of the same sample at 10,000 G. most of the larger particulate organic phosphate should be removed (Gran 1933). If a further digestion and phosphate determination is carried out on the supernatant of the centrifuged sample, the relative concentration of soluble and particulate organic phosphorus as separated by this technique can be estimated.

(ix) *Nitrate Nitrogen.*—Nitrate nitrogen was determined by a modification of Harvey's method. Details of this procedure are given in an earlier paper (Rochford 1947). Before 1947 a Klett visual colorimeter was employed for comparison of standards and samples. Since 1947 a Spekker photoelectric absorptiometer using 1 cm. cells and the Ilford 601 filters has been used. The data are entered as μg. nitrate nitrogen per litre. No salt error corrections have been applied. The routine precision of this determination is not high, and is about ± 10 per cent. in the range 0-50 μg. N/l., rising to as high as ± 20 per cent. between 300 and 500 μg. N/l.

(x) *Hydrogen Ion.*—pH has invariably been determined by an electrometric method, employing a glass electrode and a saturated calomel half cell. Buch's (1937) corrections have been applied to the data, which are recorded as *in situ* values at atmospheric pressure.

(*b*) *Mud Analysis*

(i) *Definition and Preparation of a "Silt" Suspension*

For convenience and in order to reduce the sampling error the non-random distribution of larger organisms might introduce into separate samples for analysis of each individual property, a suspension containing only mud particles below a size of 0.2 mm. was prepared from each mud sample. This suspension, called a silt suspension, and containing from 1 to 5 g. silt and colloidal mud particles per litre, was prepared by the elution of a suitable portion of the mud through a 200 mesh to the inch monel metal screen. The washings were collected in a 1,000 ml. volumetric flask and made up to full volume with distilled water.

(ii) *Phosphate Retention within Estuarine Muds*

In a normal mud, phosphate is considered to be present in the following forms:

(1) Within the pore structure or interstices of the mud there may be entrapped some inorganic phosphates deposited by metabolic activities of the organisms within the mud, or by the *in situ* breakdown of detrital organic phosphates. This phosphate, which is released by stirring of the mud or by flocculation in the laboratory, is termed the interstitial phosphate.

(2) Physically adsorbed on the surface of suitable mud particles there may be found a quantity of adsorbed phosphates, as in soil. These phosphates are capable of release from this physical bondage either by internal processes of digestion in the larger organisms, or by external modification of a micro-environment by bacteria and other microbiota. It is possible, too, that the root structure of marine plants, as in land forms (Dean and Rubins 1945), can create surface conditions suitable for the desorption and subsequent absorption into their root structure of these phosphates. In estuarine studies, considerable importance is therefore attached to this form of phosphates as a limiting factor in bottom mud productivity.

(3) A considerable quantity of phosphates in mud is bound in some insoluble inorganic or organic compounds. The more probable of these inorganic compounds are ferric and calcium phosphates, but other inorganic compounds possibly do occur. Organic phosphate compounds in the tissues of the mud biota as well as in detrital organic phosphates also occur. The total phosphate figure is composed of all these forms of phosphates, together with the adsorbed and interstitial fractions.

(iii) *Analytical Procedures*

(1) *Interstitial Phosphates.*—A 100 ml. aliquot of the silt suspension was transferred to a 250 ml. reagent bottle, and 5 ml. of saturated sodium chloride were added, the whole being well shaken, and flocculation allowed to proceed for 24 hours. At the end of this period a suitable aliquot, generally 30 ml., of the supernatant was taken, diluted to 100 ml., and the phosphate content determined. Interstitial phosphate figures are expressed as μg. phosphate phosphorus per g. of mud, as contrasted with all other determinations, which are expressed as μg. or mg. constituent per g. silt.

This transformation, from amount of constituent per 100 ml. of suspension to amount per g. of silt, was carried out by the use of a silt suspension density figure, calculated as follows: 25 ml. of silt suspension were added to a tared beaker and dried to constant weight at 150°C. The resultant difference in weight multiplied by four gave the quantity of silt in 100 ml. of silt suspension. A correction factor to transform quantity of constituent in this quantity of silt, to that in 1 g., was then calculated and used on all subsequent determinations.

By the use of a formula based upon the quantity of silt in 1 g. of mud, determined as in Subsection (7) below, the interstitial phosphate figure can be expressed in μg./g. mud units. The precision of this determination is within the range ± 5 per cent.

(2) *Adsorbed Phosphates.*—To a 100 ml. aliquot of the silt suspension in a 250 ml. reagent bottle were added 5 ml. of 1N sodium hydroxide. Flocculation was allowed to proceed for 24 hours and phosphate phosphorus was determined on a suitable aliquot of the supernatant. Adsorbed phosphate is recorded as μg. phosphate phosphorus per g. of silt. The precision

of this determination is within the range ± 5 per cent.

(3) *Total Phosphates.*—Another 100 ml. aliquot of the silt suspension was transferred to a 250 ml. flask, 2 ml. of concentrated 36 E sulphuric acid and 6 drops of 72 per cent. perchloric acid were added, and the aliquot was digested as before. From a number of tests carried out it was apparent that insignificant amounts of pyrophosphate are formed by this treatment and no after-boiling was carried out. Distilled water (100 ml.) was added, the mixture well stirred, and allowed to settle 24 hours. Phosphate phosphorus was then determined after neutralization of a suitable aliquot. Total phosphate is recorded as μg. phosphate phosphorus per g. silt. If the ferric iron concentration is high a fading of the phosphate blue is sometimes observed as the stannous chloride and ferric salts react and permit back oxidation of the molybdate blue. A re-determination on a smaller aliquot at a greater dilution overcomes this difficulty. The precision of this determination is within the range ± 5 per cent.

(4) *Total Ferric Iron.*—Ferric iron was determined colorimetrically by the use of ammonium thiocyanate. A suitable aliquot of the digestion mixture was diluted to 100 ml., 2 ml. of 10 per cent. ammonium thiocyanate were added, and the colour was determined in the Spekker absorptiometer, using Ilford 602 filters and 1 cm. cells. Ferric iron is recorded as mg. ferric iron per g. silt. The precision of this determination is within the range ± 5 per cent.

(5) *Total Nitrogen.*—Total nitrogen was determined by digestion of a 100 ml. aliquot of the suspension. Five ml. of a mixture of 1 g. selenium oxychloride in 1,000 ml. 36 E sulphuric acid, followed by 2 ml. of saturated potassium sulphate, were added to form the digestion mixture. Digestion was effected at 400°C. and continued for an hour after initial clearing. The ammonia was steam-distilled in a Parnas-Wagner apparatus (1921) into 2 per cent. boric acid. Total nitrogen values are recorded as mg. nitrogen per g. silt. The precision of this determination is within the range ± 5 per cent.

(6) *Organic Carbon.*—Organic carbon was determined by Walkley's (1935) and Walkley and Black's (1934) modification of the Schollenberger technique (1927). Ferrous sulphate (1N) stored under hydrogen was delivered through a lead amalgam reducing tower for the titration of excess dichromate. Organic carbon is recorded as mg. carbon per g. silt. The precision of this determination is within the range ± 5 per cent.

(7) *Percentage of Silt Colloidal Matter in Mud.*—A weighed portion of the mud was washed in a perfusing tower of a design similar to that of Robinson (1922) through three sieves containing monel screens of 40, 90, and 200 meshes to the inch. The washing process was continued until all material smaller than 1/200 in. had been washed through. The tared sieves were then dried to constant weight at 150°C. and the amount of mud retained was calculated. The dry weight of the mud was determined by drying 20 g. to constant weight at 150°C. The percentage of silt-colloidal

matter in the sample hereafter referred to as the silt content was then calculated, allowing for this moisture loss.

The definition of sand, silt, and colloidal material used in this paper follows that of the International Society of Soil Science (1930).

(*c*) *Plotting Procedures*

In plotting these estuarine hydrological data, a choice of conventional representations was available. However, as there was insufficient material to construct cross-sectional plottings, this method of representation was not considered. To give emphasis to the longitudinal variation in properties that are found in an estuarine mixing region, a longitudinal sectional representation was chosen in preference to any horizontal plotting procedure.

As more than one river often discharges into an estuarine system, and as the properties of the bays and inlets branching off from the main system have to be considered in any plotting presentation, the conventions that follow have been followed in the construction of these longitudinal sectional representations. When more than one river discharges into an estuarine system, that with the greater flow is selected for the primary plotting.

For the primary plotting, stations situated within the channel of the estuarine system and the selected fluviatile component are used. Channel distances of these stations from the marine boundary of the system are then estimated in miles. A longitudinal representation, employing convenient scales for channel distances and properties under consideration, is then constructed. Hydrological data from inlets and bays off the main channel and from subsidiary fluviatile components are plotted as insertions on this representation (see Stations 2, 4, 13, 15, 18, and 19 on the George's River-Botany Bay system, Fig. 18).

This method of plotting enables one to perceive not only the zonal gradient of the hydrological properties in the system, but also the relationship of adjoining bays and inlets to these gradients, and the relative contribution of rivers to the hydrological properties of the estuarine system.

In plotting such a longitudinal section, no attempt is made to correct the data for the effect of varying tidal displacement. It is evident that ideally all data should be corrected to some definite tidal phase before plotting. Although by repetition of some samples on the one survey it is possible to obtain data on the tidal displacement during a given interval of time and so correct the remaining data, certain assumptions have to be made. One must assume that the tidal rise and fall at one point in the system is representative of conditions within all the system. If necessary, of course, simultaneous tidal observations could be made at a number of points within the system. Secondly, some constant relationship between displacement in a given time interval and displacement in a full tidal cycle must be ascertained by field observations at a number of points within the system.

As a consequence of the practical difficulties entailed by the collection of this tidal information, the only system for which such correction data are available is the George's River system.

A typical calculation of the displacement correction to be applied to the chlorinity values during a relatively high freshwater discharge period is given in Appendix X. None of the data used in this present paper has, however, been corrected for tidal displacement errors.

IV. CIRCULATION AND MIXING EXCHANGES IN AUSTRALIAN ESTUARINE SYSTEMS

(*a*) *Definition of Terms*

(i) *Circulation.*—In this paper the term circulation means the processes responsible for maintaining a seaward movement of freshwater components and for the estuarine invasion by neritic waters. These circulation processes are concerned with relatively large bodies of water.

(ii) *Mixing Exchange.*—By mixing exchange is meant those processes responsible for the exchange of properties, particularly chlorinity, between the freshwater and marine components in an estuarine system. Such mixing exchanges occur chiefly between relatively small bodies of water and across definite mixing boundaries. Turbulence, by the more rapid interchange of water bodies of differing properties, facilitates such mixing exchanges, but does not alter the eventual process of mixing exchange.

(*b*) *Factors Responsible for Circulation and Mixing Exchanges*

(i) *Tidal Movement.*—The tide oscillatory movement of water masses develops turbulent exchanges between the neritic and freshwater components of the system. Tidal movement *per se* does not seem to facilitate stratification, but displaces the existing water masses *in toto*. The velocities developed in the channels of an estuarine system by such displacements maintain a high vertical turbulence, which greatly increases the rate of mixing exchanges.

(ii) *Wind.*—The stirring of estuarine waters by wind is quite considerable, but its effect is so conditioned by local features, and its persistent seasonal cycle is so variable, that no attempt has been made to include it as a constant factor in this section.

(iii) *Freshwater Isostatic Head.*—As soon as the volume of water discharged into the freshwater zone increases above the equilibrium figure (Section V (*a*) (iv) (1)), an increase in the isostatic head occurs, and develops a gravity-impelled flow towards the mouth of the system. If the isostatic head be considerable, as during a flood discharge, strong velocities and turbulent mixing will be developed in the system, regardless of tidal movement.

(iv) *Marine Isostatic Head.*—During a period of drought or minimal discharge, summer evaporation losses of water in the freshwater zone may lead to the formation of an isostatic head at the marine end of the system. This head will assist the penetration of neritic waters into the system, but the velocities developed by this process are not of sufficient magnitude to develop vertical turbulence. This marine isostatic head, however, is responsible for the extreme marine domination of the south-west estuarine systems during the summer drought period (Section V (*a*) (iv)).

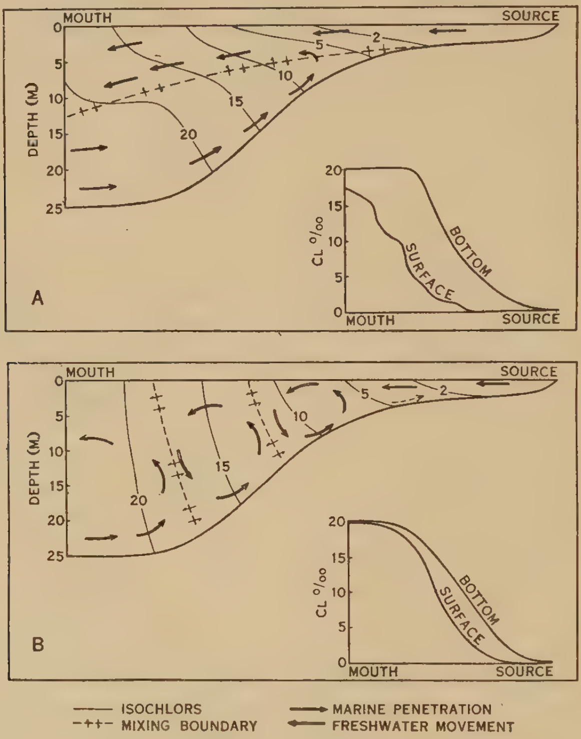

Fig. 2.—Circulation and mixing exchanges between freshwater and marine elements in Australian estuarine systems. In the upper half, the equilibrium circulation and the position of the mixing boundary in a typical atidal Western Australian system is shown, together with the type of chlorinity distribution curve associated with it. In the lower half, the equilibrium cellular circulation and position of the mixing boundary in a typical tidal eastern Australian system is shown. The insert shows the longitudinal distribution of chlorinity in such a system.

(*c*) *Mixing and Circulation in the Tidal Estuarine Systems of Eastern Australia*

In these systems the fresh water discharged during the equilibrium phase of run-off (Section V (*a*) (iv) (i)) is absorbed by the following cycle:

By dilution with the adjoining water mass, a mixed body of water is formed which develops a local cellular circulation of the type shown in Figure 2*B*. Similar cellular circulations develop at intervals along the length of the system, with mean chlorinities of each increasing to a neritic value. The absorption of the freshwater discharge then appears to take place by successive dilution exchanges across the vertical or semi-vertical mixing boundaries between these successive cellular circulations. Such mixing exchanges do not appear to be confined to any particular depth stratum.

At discharge figures above the equilibrium value, the absorption of the fresh water by this process still operates, although a seaward displacement or compression of the successive cellular circulation occurs. It is rarely that these vertical circulation cycles are completely obliterated by freshwater pressure. These circulation patterns prevent the development of stratification in eastern Australian systems, except in the extreme end of the gradient zone, where the first mixing exchange between fresh water and estuarine waters occurs.

It is important to note that this type of circulation re-circulates to the surface layers, at a rapid rate, any bottom-formed material, and also distributes the latter over a wide area of the system. Mixing exchange of material between these successive circulation cells is also a relatively simple matter in view of the vertical nature of the mixing boundary.

(*d*) *Mixing and Circulation in the Atidal Systems of South-West Australia in Which a Shallow Marine Bar is Not Developed*

In these systems the following cycle of freshwater absorption during the equilibrium phase of discharge operates:

The fresh water moves seaward as a surface layer with little mixing with adjoining surface or subsurface water masses until well down the system. The marine water masses persist as a deep sub-surface layer, and a marked halocline separates these bottom waters from the mixed surface layers. This halocline, in conjunction with the lack of tidal turbulent motion, effectively blocks any development of the vertical circulation pattern established in the eastern Australian system.

Thus the average circulation in an atidal system consists of a surface movement of diluted water masses towards the mouth, and a slow isostatic replacement of bottom water from neritic sources with mixing exchanges between them occurring along a horizontal boundary (Fig. 2*A*).

As this mixing exchange often has to occur in the absence of turbulent mixing, the process is very ineffectual by comparison with that operating in the eastern Australian system.

As the volume of fresh water discharged in such a system increases above the equilibrium figure, mixing between the surface and bottom layer progressively deepens the halocline and eventually a complete freshwater scouring of the whole system occurs (Fig. 3*A*3). The subsequent return to the normal circulation pattern is particularly slow in these atidal systems, with the neritic waters replacing isostatically (as a bottom layer) the slow loss of fresh water from the system by evaporation or seaward drift.

It is necessary to stress the importance of the effect of these two types of circulation upon productivity and zonal characteristics of the estuarine system. In the tidal type productivity is spread throughout the whole vertical range of the system, but in an atidal type, stratification develops depth productivity characteristics similar to those encountered in lacustrine studies (Welch 1935).

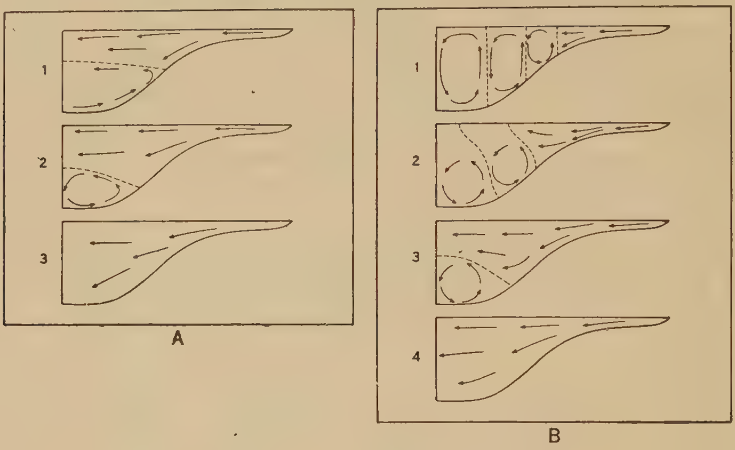

Fig. 3.—*A*. Successive stages in the freshwater scouring of an atidal estuarine system in which a shallow marine bar is not developed. *B*. Successive stages in the freshwater scouring of a tidal estuarine system.

In both (*A*) and (*B*) the dashed line represents the location of the mixing exchange boundary.

(*e*) *Development of Local Conflicts in Relation to Circulation Patterns*

In estuarine systems the greater proportion of mixing and dilution processes are effective at dimensions below that of water particles. Superimposed upon these processes, which vary in intensity with changes in freshwater and neritic pressure, there occur the horizontal translatory isostatic displacement of water masses under the influence of rhythmical tidal rise and fall of water level. The effect of such translatory movement on the diurnal variation in hydrological properties at fixed reference points within an estuarine system will be discussed in Section V (*e*). It is necessary at this juncture to stress that there is a difference between mixing and circulation patterns and these persistent diurnal variations in properties. A persistent rhythmical variation in local properties within a system is wholly dependent upon tidal energy,* but mixing exchanges and circulation are assisted, but not wholly maintained, by such energy sources.

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* Excluding wind-generated seiches, which have been observed occasionally in estuarine systems.

In the cellular type of estuarine water circulation, water bodies with narrow ranges of hydrological properties are maintained in the gradient zone. These water bodies are oscillated around a mean position by the diurnal rise and fall of tidal water level. The extent of such oscillation is termed the conflict value and can most appropriately be measured by the diurnal variation in Cl°/oo at the mean position under consideration.

(*f*) *Flood Displacement and Recovery Circulation Cycle in Tidal Systems*

As the freshwater discharge into a tidal system with a cellular circulation cycle increases above the equilibrium figure, an increase in the volume of the fast-flowing freshwater zone, accompanied by a seaward displacement of the circulatory cells, occurs (Fig. 3*B*2).

Normally, such a displacement occurs without disruption of the boundaries between these circulation cells, but occasionally the freshwater pressure is able to effect a complete scouring of the system (Fig. 3*B*3 and 4).

If the flood displacement does not proceed beyond the stage in Figure 3*B*2, restoration of the equilibrium phase is relatively simple and rapid. If, however, almost a complete freshwater scouring has occurred, restoration takes place by successive stages of longer duration. Initially in this recovery cycle stratification of the pattern encountered in the atidal system develops in the marine end, but tidal pressure of marine elements rapidly develops a cellular circulation with vertical mixing boundaries.

(*g*) *Mixing and Circulation in the Swan River System, in which a Shallow Marine Bar and a Deep Estuarine Basin are Well Developed*

In this system, the counter-circulation of neritic waters, as depicted in Figure 2*A*, is impeded by the shallow and relatively narrow channel between Station 4 and the entrance. Neritic penetration during the equilibrium phase is therefore slow, and is, in the absence of tidal energy, dependent upon a wind-generated marine isostatic head. This circulation pattern is diagrammatically represented in Figure 4*A*. During this circulation phase, the estuarine basin acts as a trap for neritic waters, which are only slowly circulated by interaction with the surface movement of freshwater elements.

During floods in this system the mixing boundary between the deep marine and surface freshwater elements becomes progressively lowered, until eventually conditions as shown in Figure 4*B* become established. In this phase the mixing boundary is below sill level, marine penetration ceases, and the basin waters become completely isolated. The surface circulation of freshwater elements is practically unimpeded.

If the flood waters increase in volume beyond this level, a complete disruption of the mixing boundary occurs and a freshwater scouring of the basin, as shown in Figure 4*C*, occurs. The restoration of this system to the equilibrium phase is rather slow, and the cycle depicted in Figure 4*D* operates as the freshwater pressure diminishes in the post-flood period.

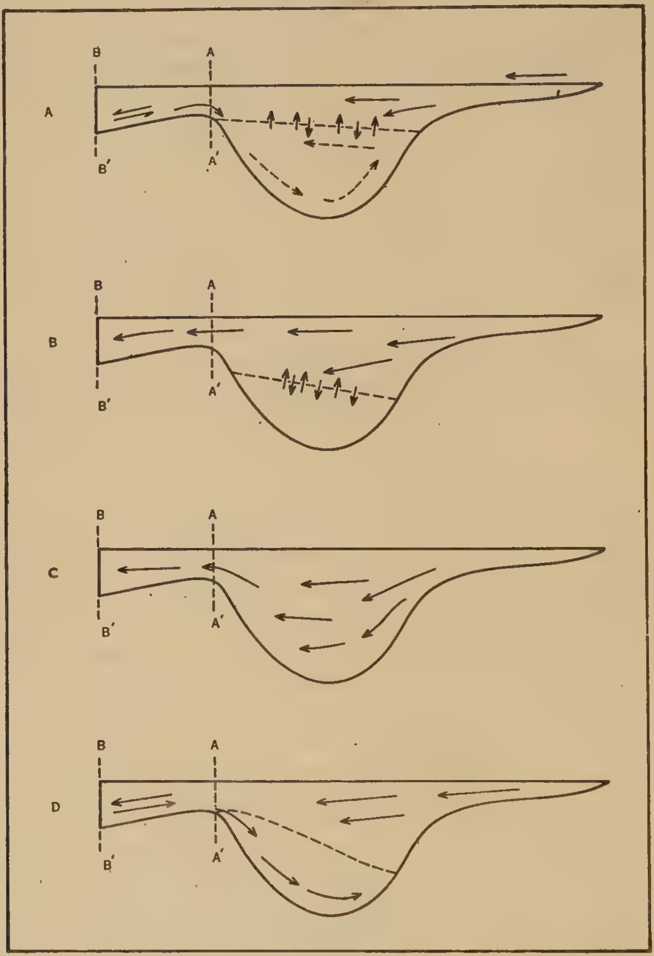

Fig. 4.—Successive stages in the freshwater scouring and the initial stage of marine penetration in the Swan River estuarine system. The dashed line again represents the position of the mixing exchange boundary.

Initially, as the freshwater pressure in the shallow entrance channel decreases, marine penetration at bottom level occurs during favourable wind sets over the adjoining neritic waters. Some of the marine water thus introduced may overflow the sill and cascade as a density current into the bottom of the estuarine basin. As the freshwater pressure still further decreases, more and more marine waters cascade into the basin, the horizontal mixing boundary is re-established, and the system slowly returns to the equilibrium condition.

V. The Estuarine Environment

(*a*) *Hydrology of Estuarine Waters*

(i) *Flow Characteristics of Australian Estuarine Systems*

The annual rainfall of Australia can be conveniently grouped into winter and summer régimes, with intergradation along the boundaries of these régimes. The upper portion of Figure 5 shows the mean Australian January and July rainfall distribution in inches. From a consideration of this rainfall distribution it is evident that the northern New South Wales estuarine systems incline more to the summer monsoonal rainfall pattern, whilst the south-western Australian systems belong to the winter rainfall pattern.

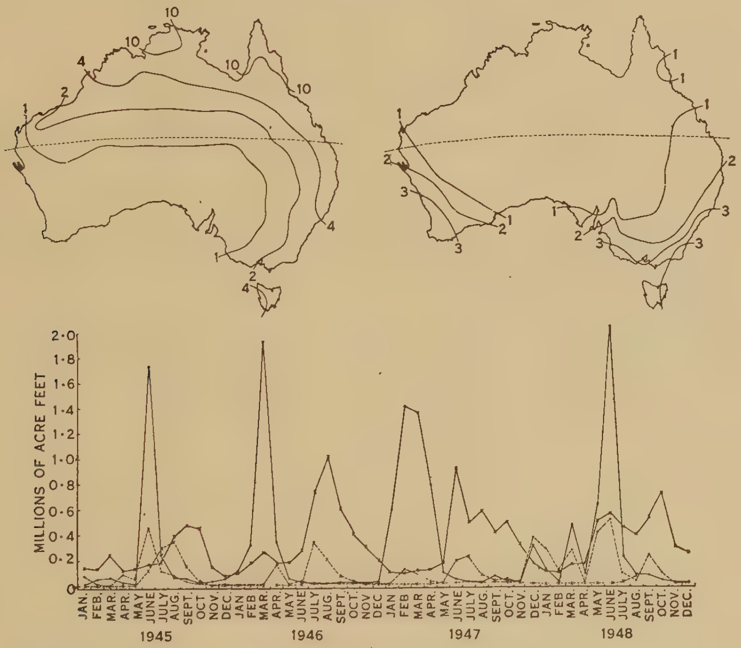

Fig. 5.—Upper left: Average distribution of mean rainfall isohyets in January. (C.S.I.R.O. 1949.)

Upper right: Average distribution of mean rainfall isohyets in July. (C.S.I.R.O. 1949.)

Lower: Comparative discharge data for the following rivers:

●—● Clarence River, N.S.W. ×—× Derwent River, Tas.

●- -● Nepean River, N.S.W. ×- -× Blackwood River, W.A.

The New South Wales, Victorian, and Tasmanian systems belong to a rainfall régime with a more evenly distributed annual pattern. In Tasmania, the presence of winter snows in the central plateau causes spring flooding and a persistent flow throughout the summer months. Selected examples of the discharge pattern of the fluviatile components of Australian estuarine systems are given in the lower portion of Figure 5.

The graph for the Clarence River, as an example of a summer rainfall régime type, demonstrates clearly the relatively enormous volume of water discharged into the northern New South Wales systems during the flood cycle, and the paucity of flow during the winter drought period. The Derwent River in Tasmania and the Blackwood River in south-western Australia are examples of the winter-flood-dominated systems with the effect of post-vernal melting of snow clearly shown in the former. The relatively small discharge of the Blackwood River is to be correlated with the relatively small winter rainfall of the south-western Australian area compared with the more continuous and heavier rainfall of the Tasmanian region. The comparatively small discharge of the Nepean River, and its extreme variability in respect of intensity and seasonal onset, are typical of central and southern New South Wales and most Victorian systems.

(ii) *Zonation Concept in Australian Estuarine Systems*

As demonstrated in (i), Australian estuarine systems fall into three primary groups:

(1) Those dominated by summer flood and winter drought discharges.

(2) Those dominated by winter flood and summer drought discharges.

(3) Those with varying discharge characteristics possessing features of both (1) and (2).

Ecologically, this grouping has some significance, especially in respect of productivity (Section VI (*a*) (ii)) but its usefulness in an attempt to formulate a satisfactory hydrological scheme of estuarine classification has been found to be very limited.

It is apparent that a scheme of classification based upon the zonal distribution of the hydrological properties of estuarine systems, and including the effect of these discharge groupings, should be the ultimate criterion and will have the maximum ecological and biological significance.

Based upon the results of the present series of investigations, a schematic representation of the zonal divisions of an ideal and somewhat symmetrical Australian estuarine system is presented in Figure 6 and the relationship of certain bottom mud properties to these zonal divisions in Figure 7.

(iii) *Discussion of Terms used in this Schematic Diagram*

An estuary is generally defined as that part of a marine inlet or brackish water environment that is subject to persistent tidal rise and fall of water level. There does not appear to be any definite relationship between the extent of marine penetration of the saline elements and the limits of such rise and fall of water level. For example, in the George's River, a considerable rise and fall of water level can be detected at the Prospect Creek station (Fig. 36), although this station is situated within the freshwater zone of this system. Again, the chlorinity of the water masses subject to tidal rise and fall in an estuary varies from almost marine to extreme brackish figures. Hydrologically, therefore, an estuary, according to this definition, has particularly diverse properties, and the use of such a term leads to difficulties in comparative studies of the hydrological and the ecological features of estuaries.

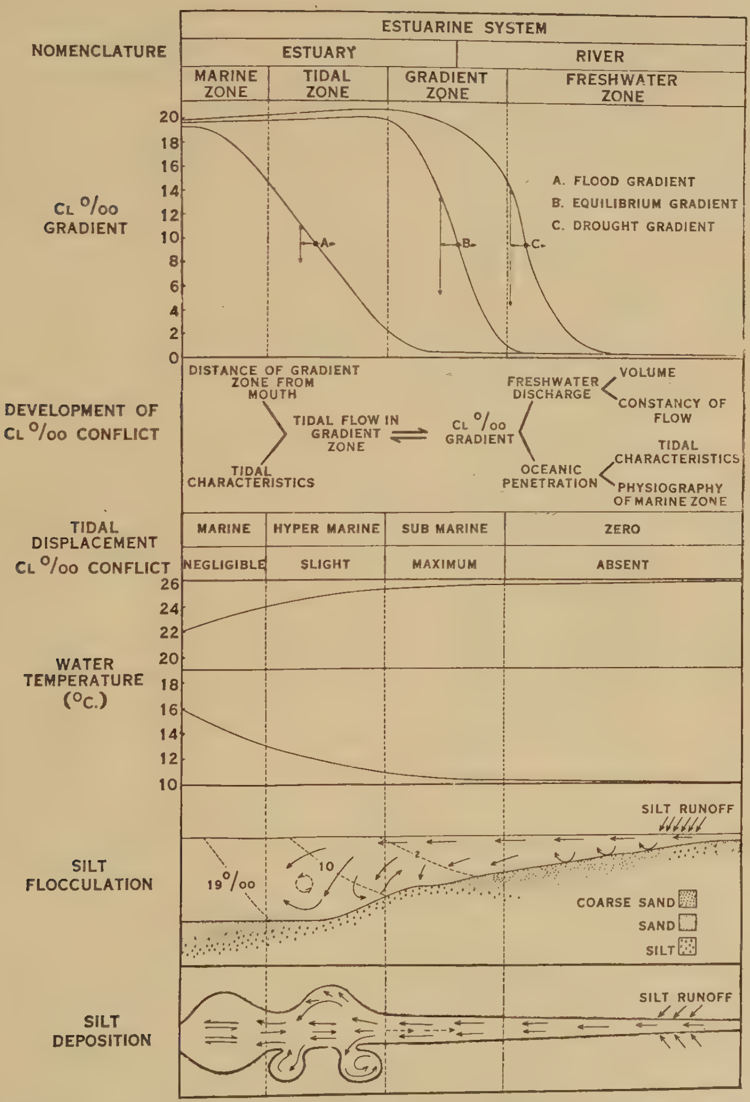

Fig. 6.—Zonal distribution of major hydrological properties in the schematic estuarine system. The temperature distributions refer to a system in latitude 35°S.

In the schematic representation here presented, the following definitions, based upon hydrological concepts, are proposed:

Estuarine system.—An estuarine complex is defined as typically consisting of a tidal compartment within which exists a system of zones (known as the estuarine system) in which marine and fluviatile elements become mixed. This complex comprises the bottom muds as well as the waters and provides habitats for biota. Its landward limit lies beyond the extreme range of penetration of the ultimate traces of the chemical and physical properties of the marine element. This limit is taken as the point within the freshwater zone at which persistent annual flow occurs.

The seaward limit of such a complex is defined as the somewhat diffuse boundary between the estuarine and neritic waters. Occasionally, therefore, the seaward boundary extends beyond the natural geographic entrance to the estuarine system, and more generally in some flow régimes the landward limit of such a system extends beyond the limits of the tidal compartment.

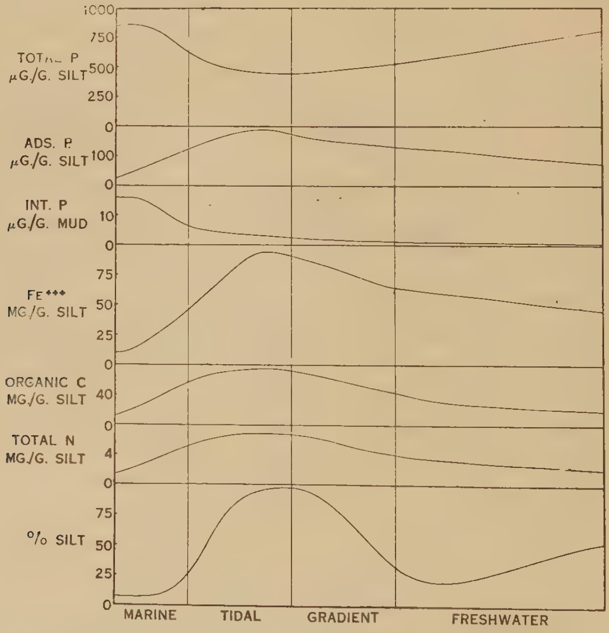

Fig. 7.—Zonal distribution of bottom mud properties in the schematic estuarine system.

In this estuarine system the following four zones can be distinguished in order from the marine boundary:

Marine Zone.—This zone occupies the region between the somewhat diffuse seaward boundary of an estuarine system and the more definite seaward boundary of the tidal zone. Because of the similarity of its properties to those of the adjoining neritic zone the term marine zone has been given to it.

Tidal Zone.—In this zone, which occupies the region landwards of the marine zone, are normally encountered the full manifestations of the tidal rise and fall of water level. The relative shallowness of this zone, especially in the bays and inlets that are most commonly found in it, leads to a marked increase in the extent of the intertidal regions and the flocculent mud flats associated with them; these are exposed during the tidal fall of water level. Because of the role usually played by tidal rise and fall in the development of the principal characteristics of this zone, the term tidal zone has been bestowed upon it.

Gradient Zone.—This zone is bounded by the tidal and freshwater zones and has been termed the gradient zone because within its boundaries occurs a transition or gradation from the almost neritic chlorinity values of the tidal zone to the fresh water of the adjoining zone.

Freshwater Zone.—This zone, which extends from the upper boundary of the gradient zone to the point of persistent flow of the fluviatile component, has been so termed for obvious reasons.

Some of the identifying properties of these zones are depicted in Figures 6 and 7 and will be discussed in detail in Section V (*c*) (i).

Conflict.—In the schematic diagram of an estuarine system in Figure 6, three Cl°/oo distribution curves have been plotted, each representing the distribution during different conditions of river discharge. The three points *A, B, C,* have been entered on these curves at the same Cl°/oo level.

If an oscillatory displacement of these curves about points *A, B,* and *C* be assumed such that each undergoes equal horizontal displacements and returns to its original position, the vertical lines drawn through these points denote the range of Cl°/oo that organisms fixed at points *A, B,* and *C* would encounter during the course of this displacement cycle. These variations in hydrological properties developed by tidal oscillatory movements of water masses in an estuarine system are termed the conflict.

The types and magnitude of conflicts thus developed will be discussed in Section V (*e*).

(iv) *Zonal Distribution of the Identifying Physical and Chemical Properties of Water and Mud in Estuarine Systems*

In this section it is proposed to give a general account of the distribution of the chemical and physical properties of the water and mud habitat in estuarine systems, followed by an examination of the actual distribution and magnitude of these properties in certain selected key estuarine systems. It is necessary to stress, however, that this section deals only with these properties in so far as they are capable of zonal differentiation in an estuarine system.

(1) *Equilibrium Discharge Phase in Estuarine Systems.*—The schematic zonal diagram presented in Figure 6 is based upon conditions prevailing during an equilibrium discharge phase. Between certain discharge levels, which are governed by the physiographic, tidal, and hydrological features of each estuarine system, a dynamically balanced state is established in which freshwater intrusion is absorbed by mixing exchanges (Section IV), without substantial or permanent displacement or distortion of the major hydrological features of the system.

Above or below this equilibrium discharge, considerable displacement of water masses occurs and flood scouring or drought saline domination is the end result of such variation in the discharge level. The rate at which each system returns to the equilibrium phase is also governed by local features. In general, however, in the eastern Australian estuarine systems, persistent tidal pressure from the marine end, aided by the cellular circulation, rapidly re-establishes the equilibrium state after flood displacement.

In the Western Australian atidal systems, the recovery phase is particularly slow and the calculation of an equilibrium discharge is accordingly difficult. Complete cessation of freshwater run-off in most eastern Australian systems is rare, and the reversion to a drought phase of distribution of hydrological properties need not be considered as different from the normal equilibrium state.

In south-western Australia, however, the rather lengthy and persistent cessation of summer and autumn run-off leads to the extreme penetration of saline water masses and further complicates the calculation of normal conditions for these systems.

(2) *Calculation of the Equilibrium Discharge in Estuarine Systems.*— If over a period of years longitudinal sampling within an estuarine system has been carried out at frequent intervals (preferably monthly at most), and there has been no marked departure of the annual discharge cycles from a normal pattern for that region (Section V (*a*) (i)), then a calculation of the grand arithmetical mean of all Cl°/oo values will approximate closely to the equilibrium values of this property. At some period during the sampling in this estuarine system, hydrological values of the same order as these equilibrium values of Cl°/oo will have been found. The discharge of fresh water into the system at this period is then taken as the equilibrium value.

It might be questioned why a direct calculation of the mean discharge figure during the same period is not accepted as the equilibrium discharge value. It has been found, however, in the George's River system that the discharge figures that are available for this purpose are not directly related to chlorinity changes in the system. In this system the area enclosed in the gradient zone by the Cl°/oo curve from a conventional longitudinal plotting for each survey has been calculated by the use of a planimeter. The following scatter diagram (Fig. 8) demonstrates the relationship between these Cl°/oo areas and the corresponding discharge figure for a gauging station on the upper George's River. Although the number of high discharge observations is insufficient to compute the exact relationship, it is evident that a curve of the exponential form as fitted to the data by eye (Fig. 8) would express the relationship between these variables. Below a discharge figure of about 1,000 million gallons per month into the George's River system, the arithmetical means of chlorinity and discharge should agree, but beyond this discharge level no simple agreement can be expected. Under these circumstances, and especially in view of the fact that gauging data are unavailable for a considerable number of estuarine systems, it was considered best to calculate the equilibrium discharge as a mean chlorinity figure and to express this in terms of actual discharge volume whenever such a transformation could be effected. This transformation can best be effected by marking on the season curves for Cl°/oo, at the selected station, the mean equilibrium Cl°/oo line. The discharge figures for the longest period during which values of Cl°/oo have been stabilized around this mean figure are then selected, and the mean of these flows is taken as the equilibrium discharge. At other periods, when the Cl°/oo is fluctuating widely about the mean value, very different and inconsistent discharge figures will be found associated with the mean Cl°/oo value.

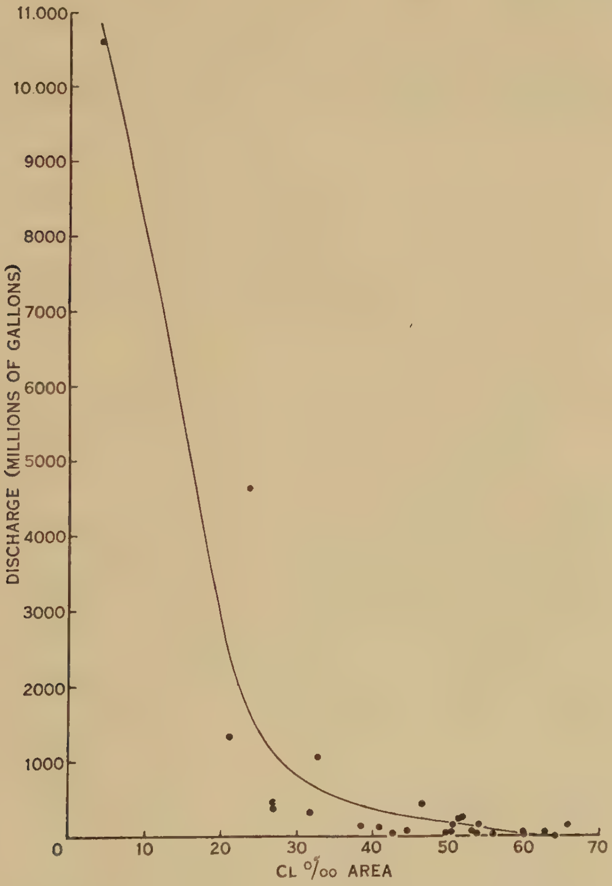

Fig. 8.—Probable form of the relationship between discharge volume and chlorinity dilution in the George's River, N.S.W.

Table 3 lists the calculation of this equilibrium value for estuarine systems for which the necessary data were available. The station selected for the mean calculation lies within the middle of the gradient zone, and the Cl°/oo value listed is a mean of the surface and bottom values.

(3) *Chlorinity.*—Chlorinity is the most satisfactory hydrological property for identifying the extent of mixing between the marine and fluviatile elements in an estuarine system. From the ecological standpoint, moreover, the absolute chlorinity distribution is a major factor in determining the limits of invasion into such a system of marine and freshwater organisms. Further, the rapid short-term conflicts in chlorinity play a significant part in the complete adaptation of organisms to a particular chlorinity level (Section IV (*d*)).

TABLE 3

EQUILIBRIUM VALUES

System	Period	Number of Observations	Mean Cl°/oo at Selected Station	Computed Equilibrium Discharge
Pt. Hacking	1944-1949	120	16.18	No discharge data
George's R.	1944-1949	60	16.45	5400 acre feet
Hawkesbury R.	1946-1949	40	9.57	4880 acre feet
Swan R.	1947-1949	26	5.6	No discharge data

The chlorinity of an estuarine system is subject to much greater variation by freshwater dilution and mixing exchanges than are other hydrological properties. Its distribution, therefore, is important in the initial determination of certain zonal boundaries in estuarine systems. The upper and lower limits of the gradient zone can be established by the Cl°/oo distribution, but only a diffuse and small-scale Cl°/oo boundary can be detected between the tidal, marine, and neritic water masses.

Generally, a fairly well-developed chlorinity gradient, with some homogeneous chlorinity waters bounding its marine end, is present in all estuarine systems. However, some estuarine systems like those in south-western Australia are encountered in which summer drought leads to the almost complete obliteration of any chlorinity gradient.

In tidal-influenced systems, little vertical stratification of chlorinity develops except as an immediate consequence of flood discharge. However, in south-western Australian estuaries, where little vertical tidal mixing takes place, pockets of high chlorinity waters may be cut off in deep basins after the winter rains, and may persist occasionally until the following winter before vertical homogeneity is established.

(4) *Temperature.*—The annual temperature cycle of the surface waters of an estuarine system follows rather closely the annual meteorological cycle of air temperature for that particular latitude. Table 4 gives the grand mean mid-depth water temperature for a number of systems at different latitudes. The agreement between the Swan River and eastern Australian systems at similar latitudes is evident.

At the marine end of an estuarine system, the annual range of surface temperature is a minimum, with a sharp rise to a nearly constant range for the remainder of the system, and with a further slight increase in the freshwater zone (Figs. 18 and 22). This variation in annual temperature range within an estuarine system is probably an effect of the decreasing volume of water, affected by heat exchanges with the atmosphere.

TABLE 4

GRAND MEAN MID-DEPTH TEMPERATURES

System	Latitude	Grand Temp. Mean
Macleay R.	31° S.	20.21
Swan R.	32° S.	19.78
Hawkesbury R.	33° 30′ S.	18.45
George's R.-Botany Bay	34° S.	18.57
Pt. Hacking	34° S.	18.70

Thus in the marine zone the amount of heat exchanged across the air-water boundary is mixed into a greater depth stratum and its influence on the temperature of this stratum is correspondingly less than in the upper zones of the system, where the depths affected by these heat exchanges are less. In the freshwater zone of an estuarine system, increase in altitude often has a pronounced effect on temperature, inducing lower than average summer and winter temperatures. The decline in the maximum and minimum temperature figure and in the annual mean for the Hawkesbury system in 1948 is typical of this effect (Fig. 25). It is to be noted, however, that the magnitude of the annual temperature range is practically unaltered. The correspondence between surface and bottom temperature conditions is governed mainly by the efficiency of the circulation processes in the system.

In most of the eastern Australian systems it is rare to find any pronounced difference between surface and bottom temperature conditions, and when any such thermal stratification does develop, its existence is rather short-lived. In the Swan River and systems with similar circulation patterns (Section IV (*g*)), pockets of bottom water may become isolated for considerable periods, and retain during these periods most of their original temperature and chlorinity characteristics. At Ravenswood on the Murray River, in the Peel-Harvey system, the following hydrological conditions were encountered on May 16, 1947:

Depth	Cl°/oo	Temp.	O_2%
Surface	1.06	15.2	86
Bottom (20 ft.)	16.64	21.8	26

The temperature and chlorinity values of the bottom waters at this station are characteristic of summer conditions and, together with the low oxygen content, suggest its isolation for some three to four months. Such isolation in a depth of 20 ft. is remarkable and could only persist in such a dynamically static system.

As mentioned previously, the annual temperature range within the marine zone of a system is a minimum for estuarine waters. It is to be expected, therefore, that in a marine-dominated estuarine system such as Port Hacking (Section V (*d*) (iii)) the annual temperature range in the vicinity of the mouth would be not appreciably higher than that of the adjoining surface neritic waters. In point of fact, as Table 5 shows, the annual temperature ranges for this system, with one exception, have been greater than, and do not show any consistent agreement with, the neritic range.

TABLE 5

ANNUAL TEMPERATURE RANGE

Year	Depth	P.H.1	P.H.4	P.H.6	P.H.8	5 miles E. of Pt. Hacking
1941	Surface	8.8	12.1	11.89	17.58	—
1942	Surface	6.52	10.22	10.44	13.00	—
1943	Surface	9.10	13.66	14.40	19.45	8.3
1944	Surface	7.30	13.55	13.48	17.15	8.5
1945	Surface	6.65	8.90	9.15	13.25	5.0
1946	Surface	9.91	9.90	9.40	13.70	7.8
1947	Surface	14.1	13.4	12.0	12.7	6.0
1948	Surface	8.6	12.2	11.95	15.8	8.0

It is possible, therefore, that the shallow, sand-barred entrance to Port Hacking permits a sluggish exchange of neritic and estuarine water masses on a scale sufficient to establish the marine properties of the system, but insufficient to prevent the development of temperature characteristics more appropriate to tidal-dominated systems. The high local turnover of phosphates at a number of stations within this system and the slow neritic movement of these phosphates (Section VI (*a*)) afford corroborative evidence of this characteristic of the system.

In the Swan River system the annual temperature range for surface waters (Fig. 31) is constant for a considerable distance from the mouth of the system. It is difficult to reconcile this with the sluggish circulation pattern of this system (Section IV (*f*)) and the isolation of bottom waters from the surface temperature exchanges with the atmosphere. It is possible, however, that circulation of the cellular pattern may develop in the lower reaches of this system during certain wind sets over the adjoining shallow neritic waters.

While it is therefore possible to detect some degree of latitudinal regularity in the distribution of annual mean temperatures in estuarine systems (Table 4), the range between winter minimum and summer maximum appears to be bound up with local characteristics in respect of depth, circulation, and physiographical features to such an extent that no systematic approach to this temperature characteristic seems possible.

On mud flats in the tidal zone in some central New South Wales estuarine systems an interesting microthermal environment is established during the winter months. Shell Point on the George's River is situated within the tidal zone, and Figure 9 gives the result of one of a continued series of observations on the mud-water temperature relationship.

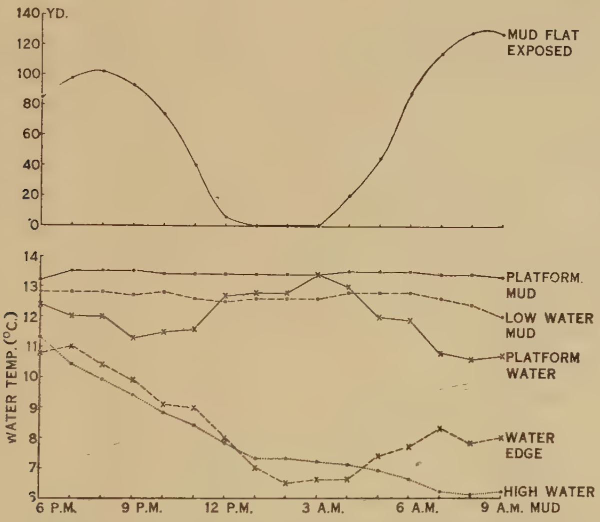

Fig. 9.—Nocturnal variation in mud and water temperature of the intertidal zone, Shell Point, George's River, on 29-30.vi.1948.

The platform referred to is at the end of a jetty extending some 200 yards over a mud flat. The other observations of mud temperature were made at distances of 120 yards from the shore, and at the shoreline just below the H.W.S. mark. The water edge temperature was taken in the first 10 feet of the tide front as it moved over the mud flat. At 6 p.m. there was found a difference of several degrees centigrade between water-mud temperatures at the platform and at the high water level. As the air temperature dropped, the mud at the high water level lost heat to the air until it was covered by the tide at about 12 midnight, from which time heat losses were minimized until about 4 a.m., when, on re-exposure of the mud to the air, heat losses again continued until almost the end of the observation period.

The water at the tide edge, advancing as a front over this rapidly cooling mud, and itself being cooled from above by the air, lost heat at almost the same rate as the mud, but on the ebbing tidal phase, possibly through dilution with warmer water nearer the low water mark and later by insolation, regained some heat. The importance of this cold front development as a factor in the environment of the intertidal zone is apparent. At about 3 a.m. there had developed a gradient of 7°C. in 150 yards over the Shell Point mud flat; and at 9 a.m. this gradient had been reduced to about 3°C. This cold front development is bound up with the phase and range of the tide. The phase of the tide determines at what stage, in the nocturnal air temperature cycle, maximum exposure of the mud flat takes place, and the range determines the extent of such mud flat exposure. Obviously, the maximum development of a cold front is possible when the advancing water edge moves over the mud flat at its lowest possible temperature.

It is considered that intertidal organisms living nearer the high water mark, experiencing greater periods of exposure to the nocturnal air temperature, which is generally less than the corresponding water temperature, are better conditioned to withstand the possible lethal effects of such a cold front. At a mid-tidal level, however, where air exposure is of smaller duration, the rapid alteration in water temperature consequent upon the passage of such a cold front could be more critical. This would apply more particularly, too, if the cold front persisted on the ebbing phase as in Figure 9 and a secondary thermal shock was suffered by these mid-tidal organisms.

(5) *Dissolved Oxygen.*—In any water mass the amount of dissolved oxygen is influenced by biological processes, viz., the photosynthetic liberation of and the respiratory demand for oxygen by living organisms, and the oxygen uptake in the chemical degradation of organic matter. During flood discharge, the oxygen consumption of the suspended colloidal soil and organic matter appears to be at a maximum near the boundary of the freshwater and gradient zones. The oxygen minimum at Station 4 on the Macleay River during the 1949 flood cycle (Fig. 30) is probably an effect of this demand. The maximum of organic phosphate at the adjoining Station 3 supports this supposition. A similar minimum in the Macleay River in January 1948 (Fig. 28) at Station 4 is also ascribable to the same organic demand.

Normally, in the surface waters of the marine and tidal zones, the oxygen content is near saturation. However, in the freshwater zone, subsaturation values are general. This characteristic, together with the minimum saturation figures of the gradient zone, develops a rather persistent oxygen saturation gradient from the marine to the freshwater end of estuarine systems. This is probably an effect of the parallel increase in the content of silt, and generally of organic matter. The annual means of surface oxygen saturation given in Figures 24, 26, 32, 34 display this oxygen zonal trend.

In the bottom waters of some estuarine systems, and particularly in the marine zone, organic matter accumulates during the spring and summer organic production outbursts (Fig. 46). In Port Hacking, the oxygen demand of this organic matter is particularly high during the late spring and summer months, and almost complete de-oxygenation of bottom waters at Station 4 has been encountered (Fig. 45).

In the marine end of the Hawkesbury River system, a similar oxygen demand occurs periodically during the year in bottom waters at Station 3 (Fig. 47), and appears to be correlated with an inorganic-organic phosphate cycle (Fig. 48). In the Swan River system, the oxygen deficiency of the bottom waters is at a maximum in the middle of the gradient zone (Fig. 34). This high oxygen deficiency is correlated with high inorganic phosphates at Station 7 (Fig. 34) and can therefore probably be ascribed to an organic decomposition cycle. In general, therefore, whilst bottom waters in eastern Australian systems display a zonal trend similar to that of surface waters, those in the marine zone exhibit a greater degree of de-oxygenation during the spring and summer production cycles.

(6) *Hydrogen Ion.*—Although the pH data are as yet comparatively restricted in quantity and scope, it is fairly clear that the normal longitudinal distribution corresponds closely with that for dissolved oxygen, with high values in the marine end of the system decreasing to minimum figures in the freshwater end. In the bottom waters of Station 3, Port Hacking, low pH values are generally associated with the dissolved oxygen minima in the spring-summer cycle (Fig. 58). Normally, too, there is a pronounced longitudinal variation in the pH of estuarine waters, values above 8.00 only occurring in the marine and lower tidal zones, and neutral or acid values in the remaining zones.

(7) *Inorganic Phosphates.*—In most Australian estuarine systems, some phosphates are discharged during floods or freshets into the freshwater zone. The actual amount of phosphates discharged into the freshwater zone by leaching from the hinterland soil varies with the volume of run-off and the chemical characteristics of the soil. In the central part of the eastern Australian system, the phosphate contributed by run-off is particularly low, and the distribution in Figures 19 and 24 is typical of this. In the waters of the estuarine systems of northern New South Wales, a high concentration of phosphates is found, and this is correlated with a high total phosphate level for the soils of this region (C.S.I.R.O. 1949). The distribution of phosphates in the Macleay River (Figs. 28 and 30) is typical of systems from these north coast regions.

In the estuarine systems of south-western Australia, a high run-off contribution of phosphates occurs during the winter-spring flood cycle. The phosphate distribution in the Swan River system (Fig. 32) illustrates this effect. In the marine-dominated Port Hacking system, there is practically no phosphate contribution by the low volume of fluviatile discharge; the maximum phosphates encountered in the middle of the system (Figs. 15 and 17) are caused by the intense local turnover of phosphates (Section VI (*a*) (iv)). Such a zonal phosphate distribution is, however, rare. Within an estuarine system in equilibrium discharge, therefore, a maximum of phosphates is to be found within the lower freshwater or middle gradient zone, with a rather steep decline to the marine zone.

(8) *Organic Phosphates.*—As mentioned in Section III (*a*), the total phosphate figure in the waters of estuarine systems contains not only inorganic and organic phosphates as such, but phosphates derived by acid digestion of the colloidal ferric phosphate and other insoluble inorganic phosphates contributed by soil leaching. As these latter types of insoluble phosphates are not directly available for intake by the estuarine fauna and flora, they should be excluded from any estimation of the total phosphates present in an estuarine water mass when productivity estimates are the ultimate object of study. Particulate or detrital phosphates, derived from local plankton turnover or introduced by mixing with adjoining water masses, are not included in this category.

In a low-discharge, marine-dominated system like Port Hacking, or in the marine zones of most estuarine systems, these colloidal insoluble forms of phosphates, contributed by leaching from the soil, should be present in insignificant amounts. In these regions of estuarine systems the organic phosphate figure, derived as a difference between the soluble inorganic and total phosphate figures, is considered therefore a reliable indicator of the amount of organically combined detrital or soluble organic phosphates in the water mass.

With these reservations, it is apparent that little zonal variation in the amount of organic phosphates occurs within the surface waters of each system (Figs. 19 and 24). In the bottom waters there is generally a maximum of organic phosphates in the marine end of the system but the absolute level varies widely from system to system (Table 10).

(9) *Nitrate Nitrogen.*—Relatively high concentrations of nitrate nitrogen are invariably discharged during the flood cycle of estuarine systems. The form of distribution shown in Figures 19, 23, 28, and 32, with pronounced maxima of nitrates in the freshwater end of the system, is typical of most systems. As well as nitrate nitrogen there is probably a high concentration of ammonium nitrogen, organic nitrogen, and some nitrite nitrogen leached out of the soil hinterland and discharged into the system by run-off.

As the work of Harvey (1940) has shown, ammonium nitrogen is often preferred as a nitrogen source by marine organisms and plants. It is probable, therefore, that nitrates only represent a part of the total nitrogen supply and do not act as limiting factors in the productivity of estuarine waters. The turnover of phosphates in the bottom waters of the Port Hacking system in the almost complete absence of nitrates (Fig. 46) is explicable on this basis.

(*b*) *Chemical Properties of Bottom Deposits*

(i) *Field Sampling Procedure*

The circulation and mixing exchanges in the waters of an estuarine system develop a reasonable degree of local homogeneity in any particular water body or stratum of that system. A water sample taken at one point can be considered a representative sample of synoptic conditions within that water mass. With bottom deposits, however, a good deal of local variation in the type of bottom deposit is found. The silt-colloidal material tends to collect in patches, the position of which is determined by the depth and circulation pattern of that region. Thus it is possible in a cross-sectional survey of an estuarine bed to find little uniformity in the distribution of silt colloidal material, although it is generally found that the channels and tidal-scoured regions are deficient in the smaller-grained, lighter types of bottom material.

The mud analyses of this study have been concentrated on the silt colloidal material of estuarine bottom deposits, and it has been the practice, therefore, to locate mud-sampling points at the muddiest portions of the beds adjacent to the water sampling station. Moreover, because the work on an intertidal mud flat at Shell Point has shown the magnitude of horizontal and vertical movement of silt colloidal mud particles in a relatively small area, it has been the practice to obtain at each station a composite sample by subsampling five times within an area of 400 sq. feet.

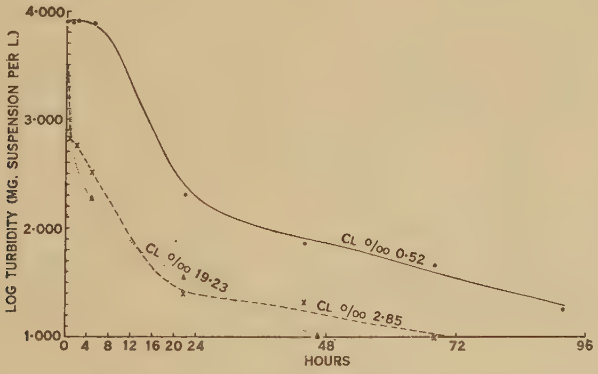

Fig. 10.—Results of a laboratory test of the settling rate of a silt suspension at various chlorinities.

Even then, considerable sampling in any one location has to be undertaken before confidence can be placed in the significance of the data in relation to average conditions in that area. The deliberate restriction of field collection to silted-colloidal bottom deposits, and the sampling error of individual samples, underlie the accuracy of the conclusions reached in the subsequent discussion of bottom mud properties.

(ii) *Silt Deposition Cycle*

In any run-off discharge from the hinterland soils of an estuarine system, and especially when such run-off is of flood dimensions, considerable quantities of eroded silt and clay materials are carried down in colloidal suspensions. Electrolytic flocculation of such colloidal material takes place at a fairly low chlorinity figure.

Figure 10 graphs the results of a laboratory test of the effect of differing Cl°/oo values on flocculation rates of a river mud suspension. In the suspension with a Cl°/oo of 0.52, little variation in turbidity occurred in the initial six hours, followed by a rapid drop in turbidity to 22 hours and succeeded in the final phase by another slow decline in turbidity to the value encountered at the end of the experiment. The acceleration in the settling velocities in the second stage of the cycle is probably an effect of electrolytic flocculation caused by the saline constituents at this extremely low Cl°/oo, followed by gravity sedimentation.

With higher chlorinities not much difference is apparent between the results obtained at a Cl°/oo of 2.85 and one of 19.23, electrolytic flocculation taking place almost immediately, and sedimentation reducing the turbidity in the first few hours to a value approximately the same as that obtained in 22 hours at a Cl°/oo of 0.52. This primary sedimentation is more rapid, possibly because of the larger size of flocculated particles involved in the process. The reduction in turbidity after the initial phase is slower and is probably governed by the smaller size and hence slower settling velocities of the flocculated particles remaining in suspension. The suspension with the Cl°/oo of 19.23 is, however, freed of all suspended matter before that with a Cl°/oo of 2.85.

As soon as flocculation occurs, the particles of suspensoid begin to settle out of the water mass. The rate of sedimentation is a balance between gravity and the vertical turbulence developed by water movement. Physical factors, such as the viscosity of the water mass, of importance in oceanic sinking rates, can be neglected in estuarine studies.

The vertical turbulence in estuarine waters is a function of tidal flow and depth of water. In the small bays and inlets, laterally placed in relation to the main channel of an estuarine system, vertical turbulence is reduced because of the reduction in the velocity of tidal flow. In addition, a closed cycle of water movement, with little contact with the main estuarine circulation, is often developed in these bays and inlets. It is in these situations in estuarine systems, therefore, that the maximum deposition of silt colloidal mud can be expected.

These sheltered bays and inlets are generally associated with the tidal and lower gradient zones of an estuarine system, and it is in these zones that maximum quantities of these silt colloidal muds are found. Any flocculated material carried into the marine zone is held in suspension by vertical turbulence until it is carried out into the adjoining oceanic waters, where it is dispersed and sedimented as the turbulence decreases. The cycle of estuarine silt deposition is schematically shown in the lower half of Figure 6. The longitudinal distribution of silt in an average estuarine system developed by these processes is depicted in Figure 7.

(iii) *Local Turnover of Phosphates in Estuarine Muds*

In Figure 11 are shown schematically the relationships between the forms of phosphates in the water and mud of an estuarine system. In the mud itself the ratio between the quantities present as interstitial and adsorbed phosphates is determined by the phosphate-absorbing power of the mud. This in turn is determined by the content of silt colloidal materials and the presence of organic complexes containing iron (Ohle 1937).

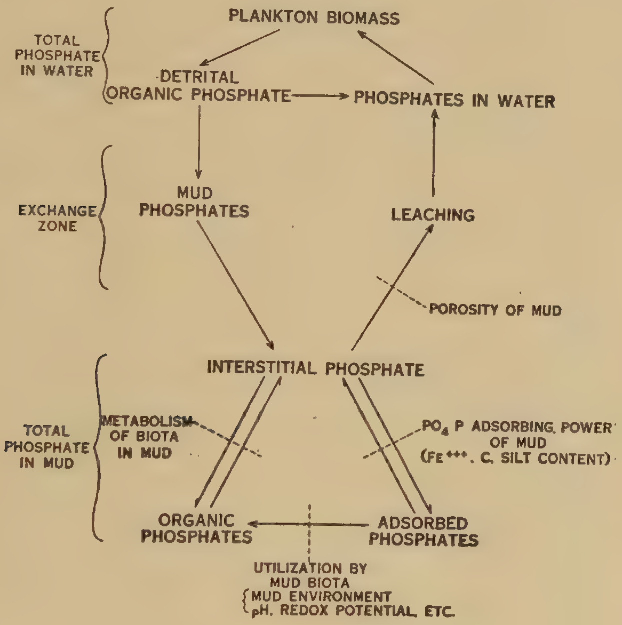

Fig. 11.—Types of and interactions between phosphates occurring in the muds and overlying water masses of estuarine systems.

Both interstitial and adsorbed phosphates are utilized by the mud biota, with the formation of organic phosphates. The phosphate uptake of the mud biota is a function of the type of organism predominating in the mud, which type is determined by the pH, redox potential, oxygen content, and other properties of the mud itself (ZoBell 1946). *In situ* degradation of these organic phosphates forms phosphates partitioned between interstitial and adsorbed forms. The interstitial phosphate is being continually leached out of the immediate surface layers, the leaching rate being determined by the porosity of the mud and the circulation of the water over the mud surface.

These leached phosphates become available for plankton utilization in the overlying water mass. As the detrital organic phosphates liberated by the degradation of this plankton fall through the water column, some are transformed into organic phosphates in the water mass itself, but a proportion is shed on to the mud surface. Degradation at this surface liberates phosphates, some of which enter into the phosphorus cycle in muds as the interstitial form.

(iv) *Chemical Properties of Estuarine Bottom Deposits in Relation to Hydrological Zones*

(1) *Interstitial Phosphates.*—As the interstitial phosphate content of a mud at any time is a dynamic balance between losses and accessions (see previous section), the interstitial phosphate in any one sample can vary considerably from an average content. However, the distribution of interstitial phosphates in Figure 7 is representative of conditions existing in an estuarine system under average conditions. The maximum concentration of interstitial phosphates is normally found within the marine zone, with some in the tidal zone, but practically none in the gradient and freshwater zones. The high content of silt muds in the gradient and tidal zones enables most of the mud phosphates to be adsorbed, so that the average content of interstitial phosphates is low. In the marine zone, on the other hand, the greater plankton turnover (Section VI) and the sandy bottom deposits favour the maintenance of a higher interstitial phosphate content.

(2) *Adsorbed Phosphates.*—In a normal estuarine system the content of adsorbed phosphates is linked with the distribution of the silt colloidal dominated bottom deposits. The distribution of adsorbed phosphate in such a system is shown in Figure 7. Maximum concentration of such phosphates occurs in the tidal and upper regions of the gradient zone.

(3) *Total Phosphates.*—The detrital phosphate contributed to the mud surface by degradation of plankton is at a maximum in the marine zone. In the freshwater zone, the bottom deposits contain considerable quantities of soil-derived organic and insoluble phosphates. In a longitudinal section in a normal estuarine system (Fig. 7), therefore, total phosphates will be found at a maximum in both the freshwater and marine zones, although their derivation in these zones is quite different.

(4) *Total Ferric Iron.*—Ferric iron compounds are introduced into an estuarine system as part of the silt colloidal run-off suspension. It is not surprising, therefore, to find that the maximum values of total ferric iron in the gradient and tidal zones are associated with the silt colloidal muds of this region. This typical distribution is shown in Figure 7. However, these studies on the annual variation in the total ferric iron content of intertidal muds demonstrate (Figs. 12 and 13) a similarity between the seasonal cycles of ferric iron, of organic carbon, and of total nitrogen. On the assumption that the amounts of these latter properties are influenced by mud biota, there is a reasonable probability that ferric iron is also similarly influenced. The relationship between bacteria and the redox potential of muds (Zobell 1946) and the diatom requirements of ferric iron (Harvey 1934) provide some indication as to how this association might be developed.

(5) *Organic Carbon.*—Carbon as determined by the technique of Schollenberger (Section III (*b*)) can exist in a number of organic compounds in bottom muds. Associated with the silt colloidal run-off suspension we may expect to find a preponderance of the soil humate complexes

with a relatively high content of carbon (Waksmann 1933). By flocculation of the accompanying silt colloidal run-off suspension, these soil humates will be concentrated in the bottom muds of the upper gradient and tidal zones of an estuarine system. A high carbon content of these muds is therefore persistently found, and the longitudinal distribution for an average system, as shown in Figure 7, displays this trend.

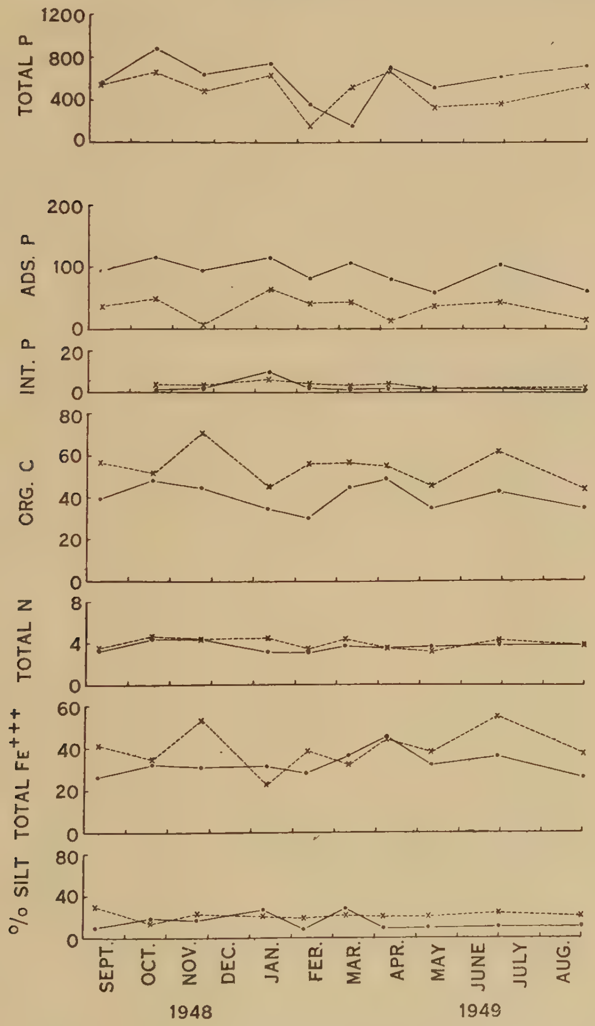

Fig. 12.—Seasonal cycle of mud properties, Shell Point, Station 6, 1948-49.

● — ● Surface data. × - - × 2 ft. data.

The plankton detritus shed on the bottom muds of the marine zone contains organic protein complexes, of a more simple nature, in association with some carbohydrate material and organic phosphates. The organic carbon deposited in the muds of the marine zone is subject to considerable annual variation in amount and is to be related to the degree of planktonic activity in the overlying water mass itself (Section VI (*b*) (iii)).

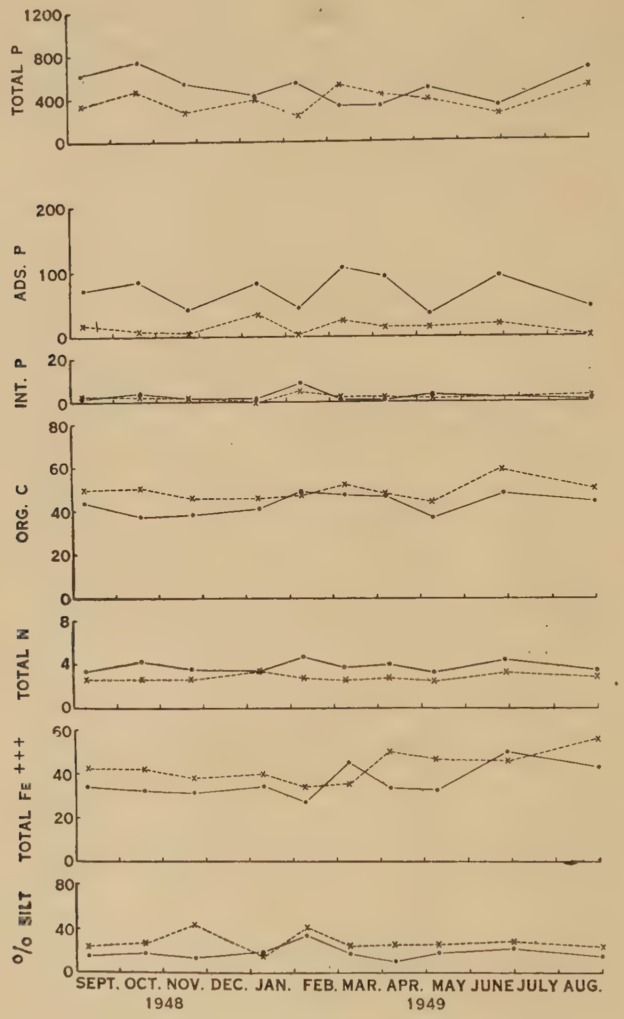

Fig. 13.—Seasonal cycle of mud properties, Shell Point, Station 12, 1948-49.

● — ● Surface data. × - - × 2 ft. data.

It is difficult to decide what proportion of the total organic carbon content of an estuarine mud is formed by local biological fixation of elementary carbon compounds, and hence acts as a measure of such biological activity, and what proportion is shed into these muds as preformed complex carbon compounds from the overlying water mass, or is derived from edaphic sources and acts as a stimulant to biological activity only.

(6) *Total Nitrogen.*—The nitrogen content of soil humate complexes is low, the C/N ratio for an average soil humate being in the region of 20 (Waksmann 1933; McLean 1930). For plankton the C/N ratio is of the order of 10 (Fleming 1940). The varying contribution to the estuarine bottom muds by soil and plankton sources of organic material should therefore develop a longitudinal variation in the C/N ratio of the latter. Table 6 shows the average C/N ratio, arranged according to hydrological zones in certain Australian estuarine systems.

TABLE 6

C/N RATIOS IN VARIOUS ZONES

System	Marine Zone	Tidal Zone	Gradient Zone	Freshwater Zone
George's R.-Botany Bay	12.6	—	10.7	17.6
Pt. Hacking	14.3	—	22.0	—
Hawkesbury R.	—	13.58	17.6	16.5

In these systems there is in evidence a consistent zonal variation in the C/N ratio, developed by the preponderance of soil organic complexes in the freshwater zone and of planktonic detrital organic matter in the marine zone. There is, however, no consistent zonal variation in the absolute amounts of nitrogen, these levels probably being determined by the operation of local factors that do not conform to the hydrological zonal pattern.

(v) *Variation of the Properties of Bottom Deposits with Depth*

In a mud profile in the Bristol Channel, Moore (1930) was able to distinguish a number of zones: an upper zone containing much organic matter and dark in colour, an intermediate reduced zone containing much less organic matter, and an anaerobic primary or parent layer with practically no organic matter. While no such profile examinations have been made in this study, the simultaneous variations of mud properties at the surface (0-3 in.) and at depths of 2 ft. have been observed for some years in intertidal muds at Shell Point, George's River. Typical results of such sampling for one year are shown in Figures 12 and 13. These results show quite clearly that:

(1) Phosphates in either the total or adsorbed forms, and generally in the interstitial form, are at a much higher concentration in the surface layer.

(2) This parallels the distribution of total nitrogen, but not of organic carbon, of which at all times the concentration in the bottom layer is equal to or greater than that in the surface layer.

(3) Some of the variations in total ferric iron can be related to similar variations in organic carbon.

(4) Whilst the silt content at Station 6, Figure 12, at the 2 ft. level remained almost unchanged during the period, at Station 12, Figure 13, a considerable degree of annual variation occurred.

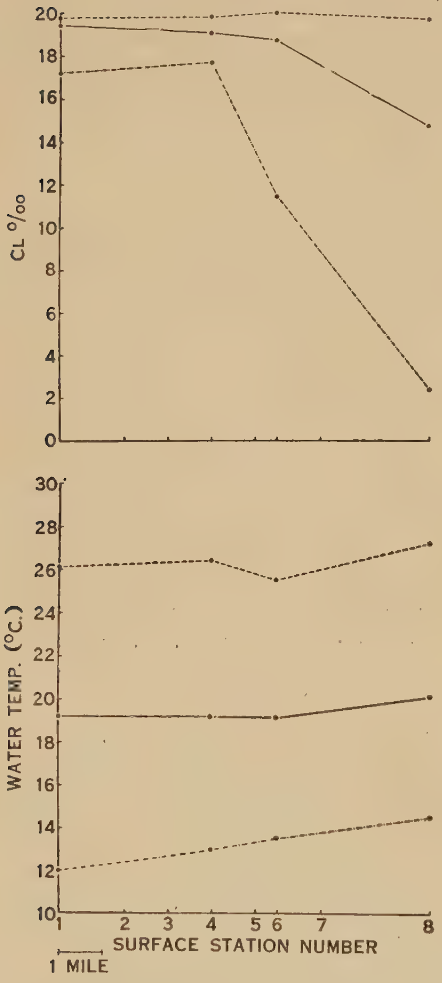

Fig. 14

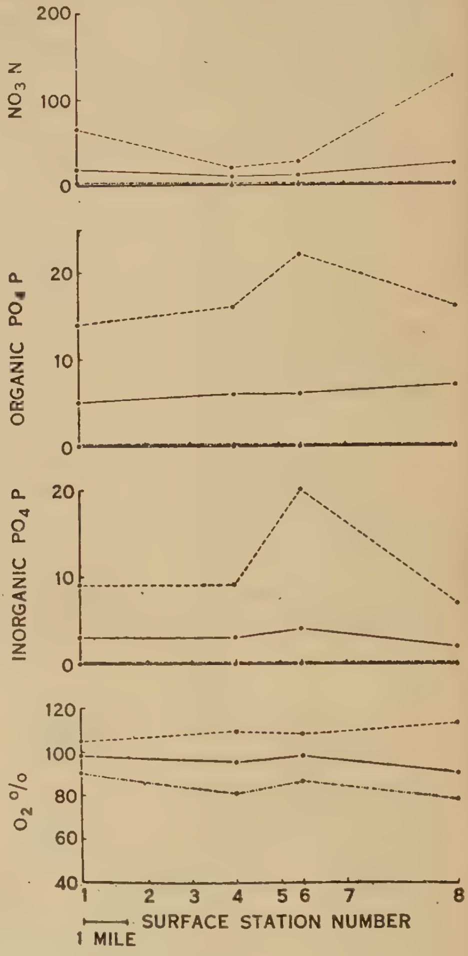

Fig. 15

Fig. 14.—Surface mean, maximum, and minimum values of chlorinity and temperature for all 1947 data in Port Hacking. In this figure and in all subsequent similar longitudinal plottings the base scale is in miles.

Fig. 15.—Surface mean, maximum, and minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1947 data in Port Hacking.

The greater concentration of the phosphate, nitrogen, and carbon constituents at the surface might be considered as evidence that a significant part of these constituents has been contributed by plankton detritus from the overlying water. Otherwise we would have expected successive sedimentary depositions of such material during floods to have established a more homogeneous profile.

On the other hand, the activities of the mud microbiota might gradually concentrate such constituents from the mud itself into the surface layer. Moreover, although the positions of these stations were chosen to yield results which could be considered as normal for intertidal muds, they were included in a comprehensive programme involving the addition of phosphatic and organic materials to experimental stations in he same region, and there is a possibility that some contamination might have occurred.

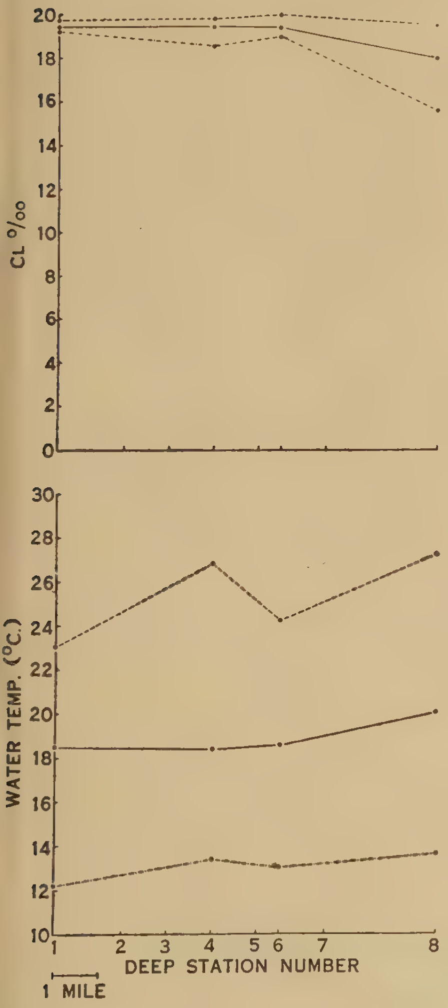

Fig. 16

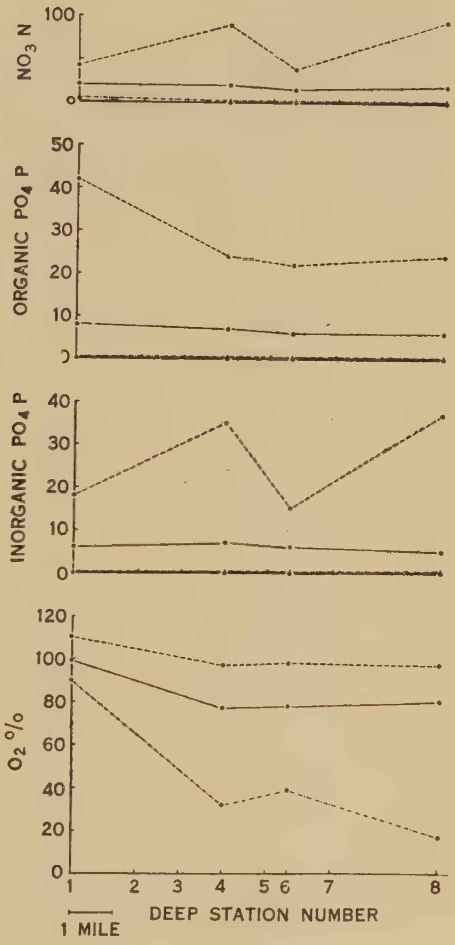

Fig. 17

Fig. 16.—Bottom mean, maximum, and minimum values of chlorinity and temperature for all 1947 data in Port Hacking.

Fig 17.—Bottom mean, maximum, and minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1947 data in Port Hacking.

In Section 6 (*b*) (iii) an examination is made of the correspondence between cycles of constituents in the mud and in the overlying water mass.

(vi) *Derivation of Constituents of Estuarine Bottom Deposits*

The high concentration of total nitrogen, phosphates, and organic carbon in marine zone muds (Section V (*b*)) and the relatively low amounts in gradient zone or freshwater zone dominated systems (Section V (*c*) (v) and (vi)) suggest that there is an accumulation of such materials from the overlying water in the marine region.

It is considered that, in the marine zone, the return of phosphates to the overlying water via the leaching cycle (Fig. 11) is less than the amount contributed by the detrital planktonic phosphates over a period of time. Phosphates, and hence the nitrogen and carbon constituents, presumably accumulate, by reason of this unbalanced cycle, in the marine muds of an estuarine system.

TABLE 7

ADSORBED P IN FLOOD WATERS

Station	Date	Turbidity (g./100 ml.)	Adsorbed P (μg./g. suspension)
Hawkesbury R. 16	23.iv.46	0.04	0
Hawkesbury R. 15	23.iv.46	0.04	0
Hawkesbury R. 14	23.iv.46	0.032	0
Hawkesbury R. 13	23.iv.46	0.032	0
Hawkesbury R. 12	23.iv.46	0.027	0
Hawkesbury R. 10	23.iv.46	0.027	0
George's R. 16	21.iv.46	0.05	14μg
George's R. 17	21.iv.46	0.08	42μg
George's R. 19	22.iv.46	0.032	84μg
George's R. 21	22.iv.46	0.032	0

In the more intensely scoured gradient and freshwater zones, the removal rate of such constituents is probably much greater and, moreover, the detrital plankton additions are smaller, if not negligible. The low nitrogen and carbon contents of the muds of the north coast system of New South Wales are attributable to a combination of scouring and of plankton inactivity in the overlying waters (Table 12). An example of the actual amounts of phosphates in the adsorbed form contributed by present day run-off to the central New South Wales estuarine systems is given by the figures in Table 7.

In the Hawkesbury River system, no adsorbed phosphates associated with the silt colloidal soil particles in the water could be detected. In the George's River, the only two water samples containing considerable quantities of phosphates adsorbed on suspended soil particles were from a region subject to considerable industrial pollution.

It is reasonable to expect, therefore, that some of the adsorbed phosphates have been introduced into the water as industrial pollutants and not from any edaphic source. Therefore, in this system, too, it is probable that the present-day edaphic contribution of adsorbed phosphates to the bottom deposits, per medium of the silt deposition cycle of Section V (*b*) (ii), is negligible. Hence, if in these systems phosphates from these bottom deposits are utilized by oysters (Section VIII), then presumably the carrying capacity of the systems for such oyster stocks could undergo a long-term secular decline.

(*c*) *Classification of Estuarine Systems on the Basis of Zonation Displayed*

(i) *Identifying Properties of the Zones*

Marine zone.—The marine zone can best be identified by the following:

(1) Hydrological properties, especially chlorinity, temperature, and nutrient salts, are subject to similar seasonal cycles as occur in the adjacent neritic waters. A persistent spring-summer turnover of phosphates is a normal feature of the waters of this zone.

(2) Absence of diurnal Cl°/oo conflict.

(3) Relatively deep water and only small areas subject to tidal exposure.

(4) Bottom deposits largely composed of marine sands overlying black mud in some areas.

(5) Bottom muds characterized by high total and interstitial phosphorus with low adsorbed phosphate values. The carbon and nitrogen contents are generally high.

Tidal zone.—(1) Nutrient salts are subject to seasonal cycles similar to those in the marine zone, but at a lower level of turnover. Temperature and chlorinity undergo greater seasonal variation, but with mean values not very different from those of the marine zone.

(2) Slight development of diurnal Cl°/oo conflict.

(3) Relatively shallow water with extensive development of intertidal mud flats and shallow bays.

(4) Bottom deposits, except in the scoured channels, principally composed of flocculent black mud with little or no sand.

(5) Bottom muds characterized by high content of adsorbed phosphate, total ferric iron, organic carbon, and total nitrogen. Productivity turnover largely concentrated in the mud-water boundary zone.

Gradient zone.—(1) Seasonal cycles in nutrient salts not very marked.

Chlorinity properties very much influenced by freshwater discharge and varying from tidal to freshwater zone values. Region of environmental insecurity, as is often made apparent by sub-saturation oxygen figures.

(2) Diurnal Cl°/oo conflict developed to a maximum.

(3) Water confined to relatively narrow channels.

(4) Bottom deposits varying from coarse sand to flocculent muds.

(5) Bottom muds characterized by properties rather similar to those of tidal zone muds, but with greater degree of variability.

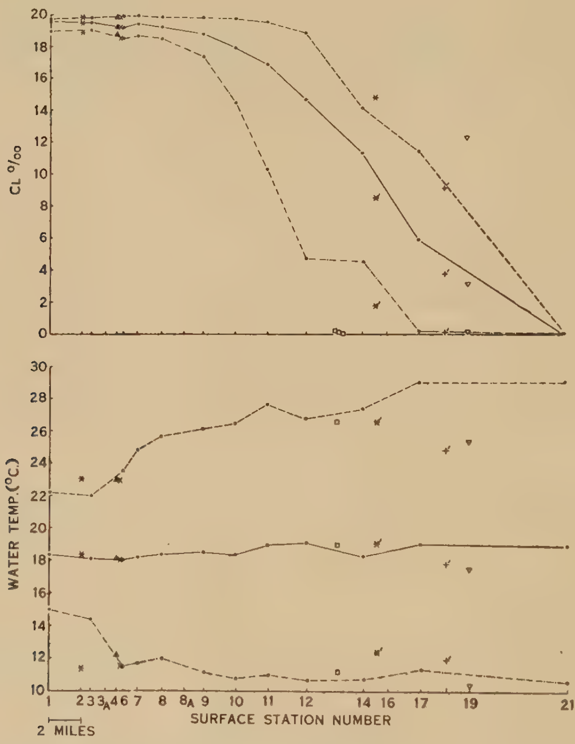

Fig. 18.—Surface mean, maximum, and minimum values of chlorinity and temperature for all 1947 data in George's River and Botany Bay.

Freshwater zone.—(1) Annual cycles of nutrients of the marine zone type are not a feature of the freshwater zone. Normally an excess of nutrients, especially of nitrates, is found in this zone.

(2) By definition (Section IV (*d*)), no diurnal conflict is present in this zone, although, in the less rapidly flowing regions of the zone, a diurnal temperature cycle is often encountered, with maximum figures in the early afternoon and minimum figures in the period before sunrise.

(3) Water confined to relatively small channels, with development of rapids and scoured basins.

(4) Bottom deposits largely composed of particles varying in dimensions from very coarse sand to small boulder dimensions.

(5) Bottom muds characterized by relatively high total and adsorbed phosphates but deficient in ferric iron, organic carbon, and total nitrogen.

(ii) *The Concept of Zonal Dominance in Estuarine Systems*

A particular estuarine system may be designated or classified according to the zone that occupies the greatest volume of the entire system. It will naturally be necessary to determine, during the equilibrium phase of such a system, the position of the boundaries of the various hydrological zones as defined in the previous section. The volume of water between such boundaries is then calculated. Unfortunately, few or no bathymetric data are available for most estuarine systems and the calculation of volumes occupied by the hydrological zones is impossible. However, in the examples to follow, where no volume calculations are available, the zonal dominance is so evident as to enable a classification to be postulated.

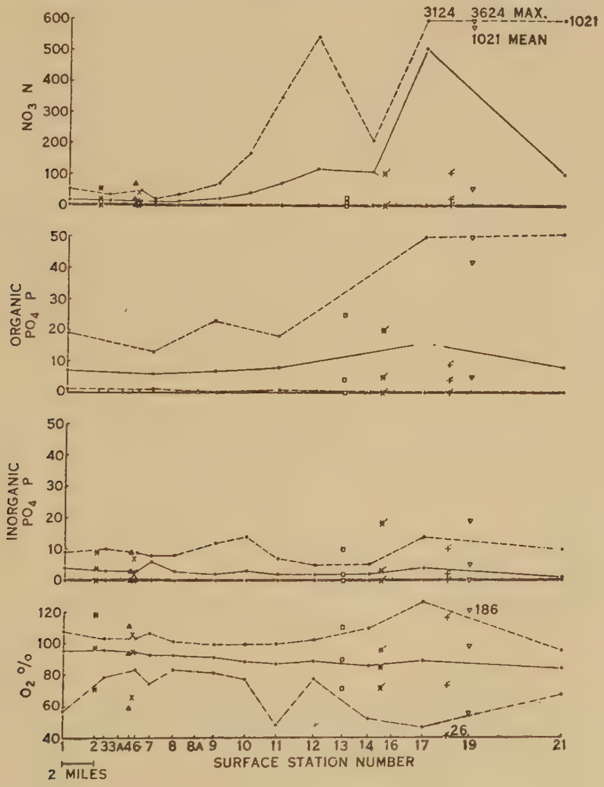

Fig. 19.—Surface mean, maximum, and minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1947 data in George's River and Botany Bay.

(iii) *Hydrological Zones in Port Hacking*

Figures 14 to 17 give in a longitudinal representation the distribution of annual means of hydrological properties in Port Hacking during 1947. The location of the station numbers is given in Appendix I. The small annual variation in chlorinity both in surface and bottom waters between Stations 1 and 6 (Figs. 14 and 16), together with the nature of the bottom deposits (Fig. 62), the annual trends exhibited by the nutrient salts at Station 4 (Fig. 46), and the absence of chlorinity conflicts within this area (Figs. 36 and 40), clearly enable us to classify this area as marine.

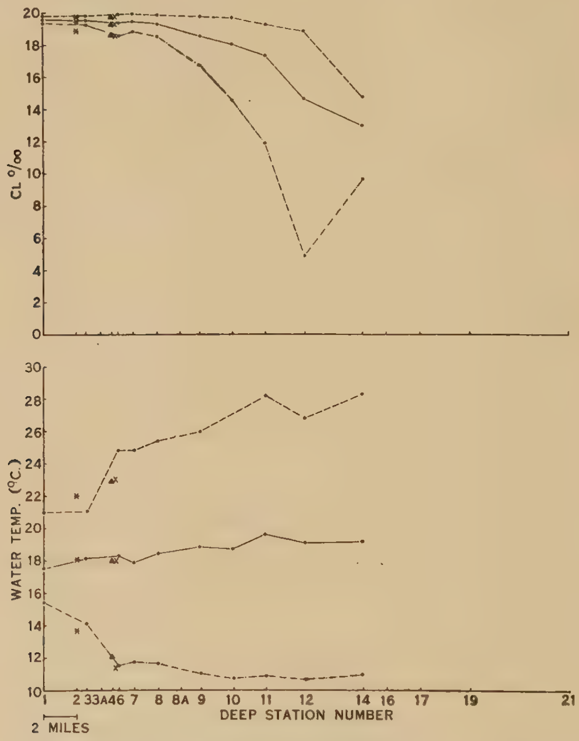

Fig. 20.—Bottom mean, maximum, and minimum values of chlorinity and temperature for all 1947 data in George's River and Botany Bay.

Because of a weir at Station 8, the continuous discharge of fresh water is impeded and the absence of a clearly defined freshwater and gradient zone is explicable on this account. Between Stations 6 and 8 there is some development of tidal flats normally associated with the tidal zone. The properties of the muds in this region lie within the range of the properties of tidal zone bottom deposits.

The annual variation in the properties of bottom deposits at Station 4 (Fig. 62), with its relatively high total phosphate and rather low adsorbed phosphate figures, supports the marine classification of the area between Stations 1 and 6.

(iv) *Hydrological Zones in George's River-Botany Bay*

Figures 18 to 21 depict the longitudinal distribution of the annual means of hydrological properties in the George's River-Botany Bay system during 1947. The station locations are given in Appendix II. Between Stations 1 and 9 the longitudinal variation in chlorinity was only slight, and this fact, together with the small annual variation at each of the stations in this area, supports the classification of the latter as the marine-idal zone of the system. The boundary of the marine zone in this system as been fixed at Station 3 and lies approximately along the 10° range line n Figure 22. This boundary has been determined largely by the marine roperties of the bottom deposits at Station 1, in which are found a ersistent low ferric iron, high total phosphate, and low silt content during

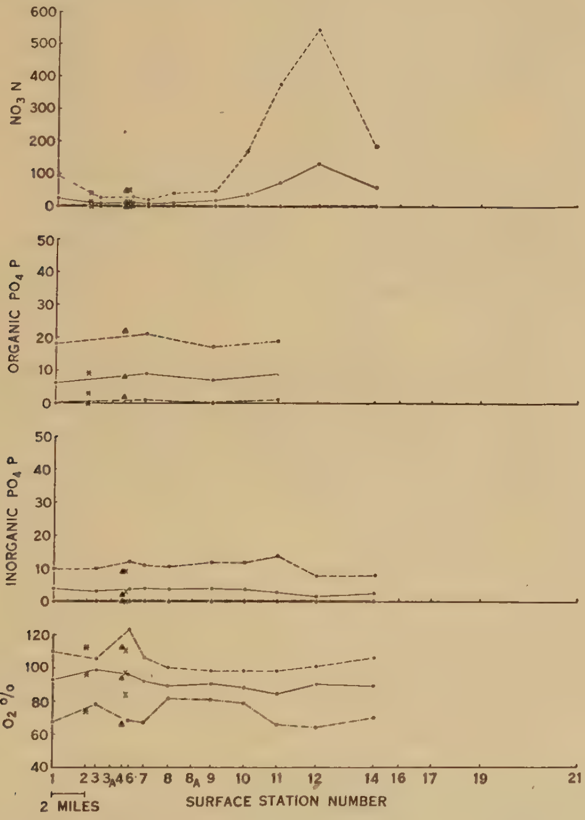

Fig. 21.—Bottom mean, maximum, and minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1947 data in George's River and Botany Bay.

an annual cycle. The relative smallness of the marine zone is apparent from Figure 22. The area between Stations 3 and 9 is classified as tidal on account of the large development of shallow bays and inlets on its south side, with extensive tidal mud flats whose chemical properties are typified by Shell Point data (Figs. 12 and 13).

The gradient zone occupies the region of the system between Stations 9 and 21. A weir between Stations 17 and 21 renders it impossible to fix the lower freshwater boundary exactly, but it lies nearer to Station 17 that is indicated by the chlorinity data.

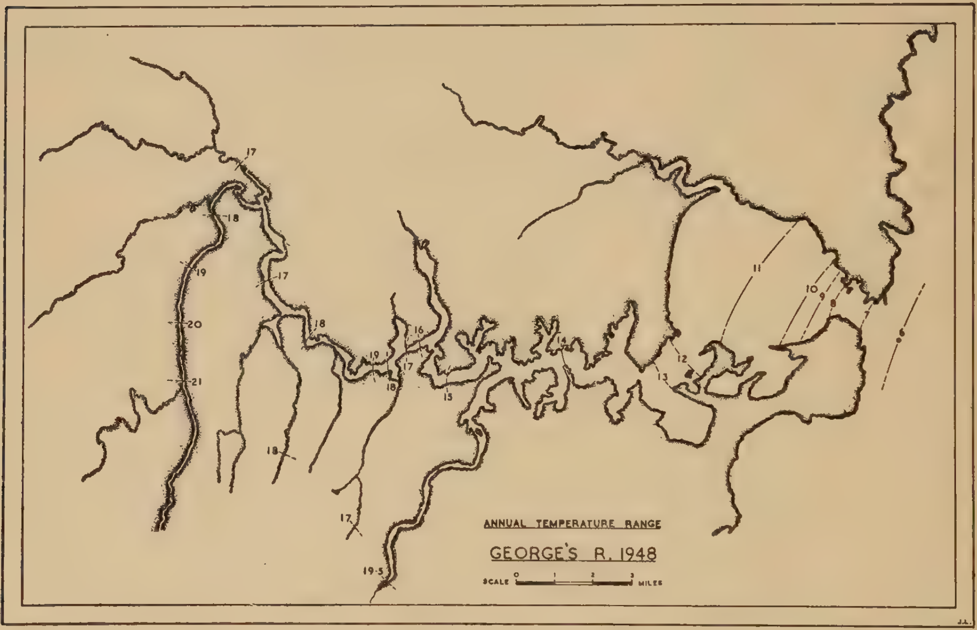

Fig. 22.—Annual temperature ranges in the George's River and Botany Bay system in 1948.

(v) *Hydrological Zones in the Hawkesbury River*

Figures 23 to 26 give the distribution of the annual means of hydrological properties in the Hawkesbury River system during 1948. The positions of the sampling stations are given in Appendix III. On the evidence of the mean chlorinity distribution shown in Figures 23 and 25, there is no marine or tidal zone in the channel section of this system. The magnitude of the gradient zone, which is about 50 miles long, is the chief feature of chlorinity distribution. The sandy bottom muds at Station 1 belong to the marine type, with low ferric iron and adsorbed phosphates but high total and interstitial phosphates.

However, the inlets on the southern side of the Hawkesbury River, of which Station 3 is a typical example, possess certain tidal zone characteristics. The existence and magnitude of the annual nutrient cycle at Station 3 (Fig. 48), together with the sub-neritic chlorinity values (Fig. 47), furnish evidence of this. However, the bottom muds at Station 3 (Fig. 63), with their high total and interstitial phosphates and low ferric iron content, are more marine in type. Nevertheless, their high adsorbed phosphate and silt content justify rather a tidal or gradient zone classification.

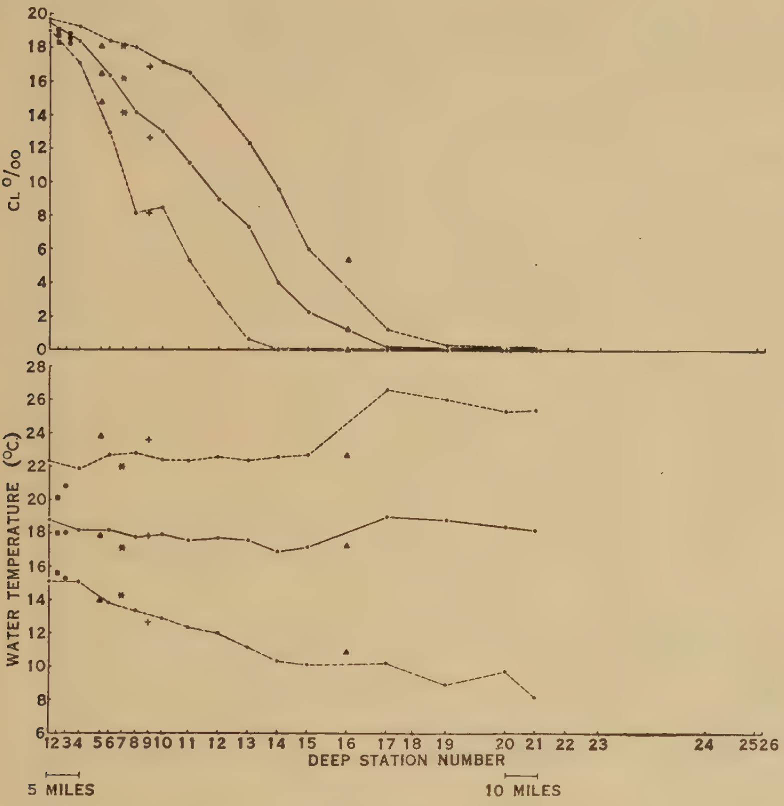

Fig. 23.—Surface mean and maximum-minimum values of chlorinity and temperature for all 1948 data in the Hawkesbury River.

The inlets on the southern side of the Hawkesbury River system have therefore been classified as belonging to the tidal zone of the Hawkesbury River. Apart from these stations, however, the hydrological gradient zone extends from Station 1 at the mouth to Station 17, with the bottom muds at the mouth possessing certain marine characteristics.

(vi) *Hydrological Zones in the Macleay River*

Figures 27 and 28 give the distribution of surface properties in the Macleay River during a low discharge period, and Figures 29 and 30 the distribution immediately following a flood discharge. The absence of any marine or tidal zone is evident from the chlorinity distribution, whilst the freshwater domination is evident from the steepness of the chlorinity gradient even during a low discharge period. The persistently low chlorinity figures encountered at Station 2 during 1949 (Fig. 52) are further evidence of the freshwater domination.

Although there appears to be a pronounced annual cycle in the bottom mud properties at Station 2 (Fig. 65), in general the adsorbed phosphate and ferric iron contents are high and the total phosphates are low. A regular decrease is apparent in the silt content, from the February floods to the end of 1949. The effect of silt deposition on these properties is discussed in Section V (*b*) (iii). These properties are tidal or gradient in zonal characterization.

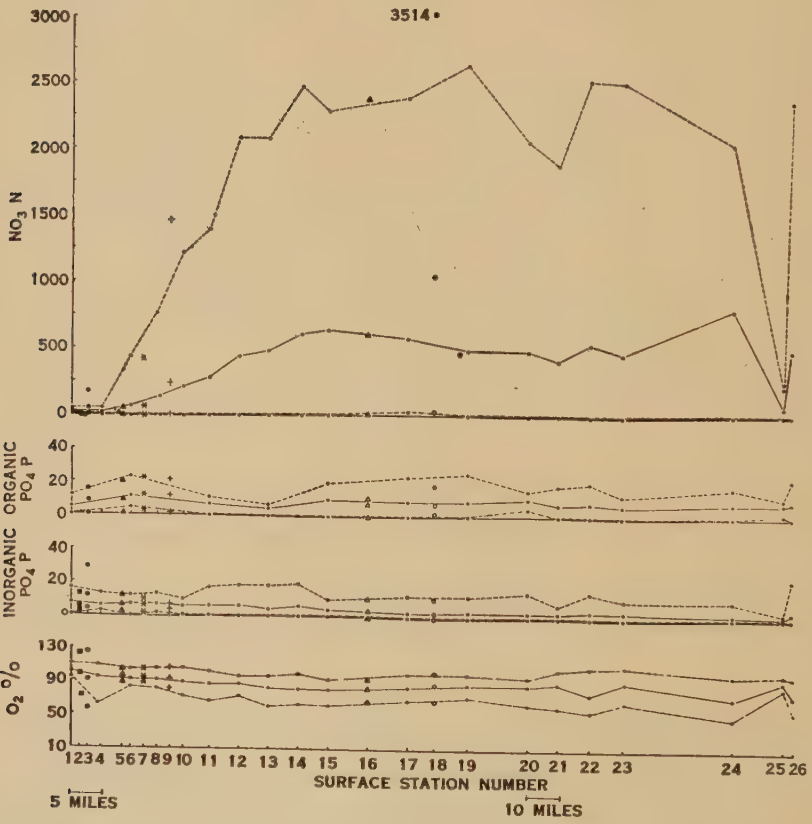

Fig. 24.—Surface mean and maximum-minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1948 data in the Hawkesbury River.

The low organic carbon content of the muds at this station is typical of muds from the whole of the north coast systems of New South Wales. As suggested later (Section VI (*a*) (iii)) it is probable that freshwater domination prevents the establishment of a plankton community able to fix the nutrients in the water, and prevents the completion of the cycle of organic detrital transfer from the water to the mud (Fig. 11).

In the Macleay River system, therefore, the gradient zone lies between Stations 2 and 4 during the normal equilibrium phase, but is displaced seawards during the comparatively short flood period each year. The remainder of the system belongs to the freshwater zone.

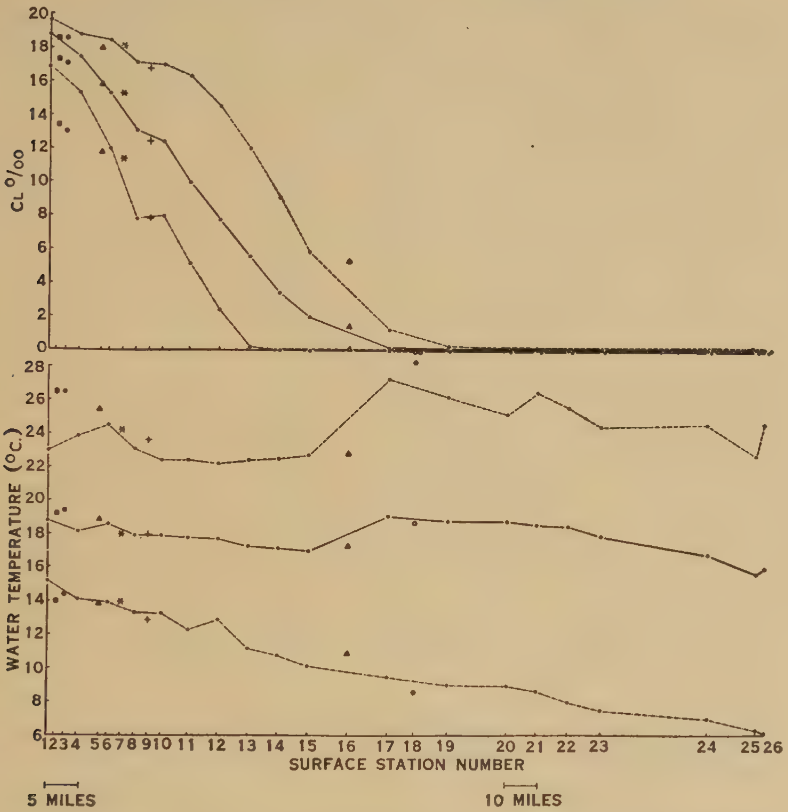

Fig. 25.—Bottom mean and maximum-minimum values of chlorinity and temperature for all 1948 data in the Hawkesbury River.

(vii) *Hydrological Zones in the Swan River*

Figures 31 to 34 give the longitudinal distribution of the annual means of hydrological properties in the Swan River system during 1947. The difference between the surface chlorinity distribution curve for the Swan River in Figure 31 and for George's River-Botany Bay in Figure 18 is particularly interesting. In the latter system the Cl°/oo curve has the appearance of being under tension from the marine end of the system, so that the asymptotic level is found at the marine end. The Swan River curve, on the other hand, is almost a complete inversion of this, with little evident pressure from the marine and most, if not all, from the freshwater end of the system. An asymptotic level is partly developed between Stations 9 and 13.

In the bottom zone the isolation of the waters in the middle basin of the system is quite apparent (Fig. 33). From the minimum figures it is to be noted, however, that almost complete flood scouring of this basin occurs. The post-flood recovery phase of this system is rather slow, and the annual cycle of chlorinity at Station 3 within the basin is indicative of this (Fig. 54). During the winter floods of 1947 and 1948, large quantities of phosphates and nitrates (Fig. 55) were discharged into the middle region of the system, but these had almost completely disappeared by the beginning of the following summer.

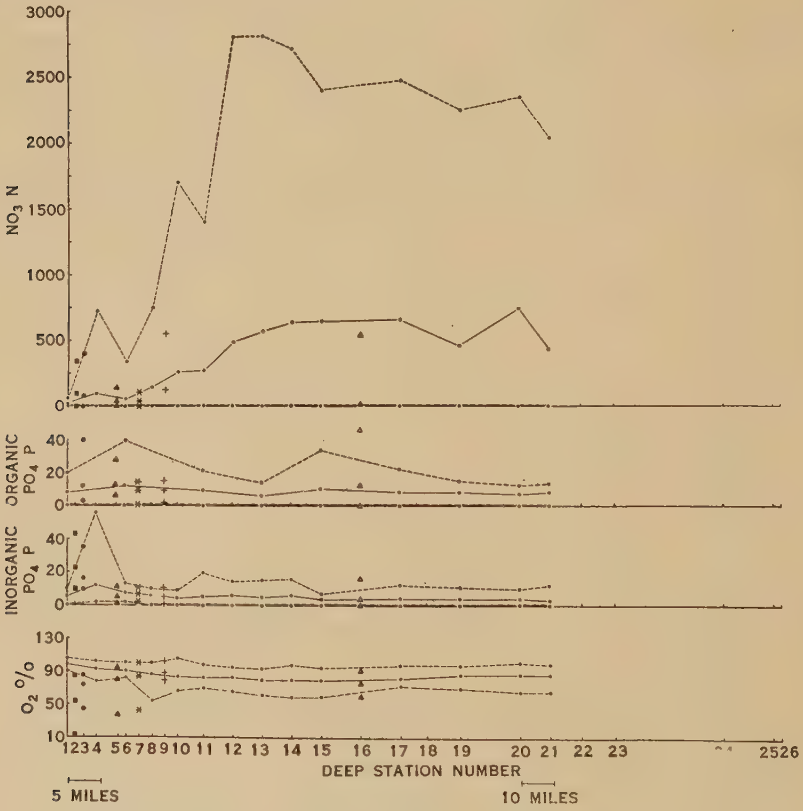

Fig. 26.—Bottom mean and maximum-minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1948 data in the Hawkesbury River.

The absence of a continuous summer turnover of phosphates, such as occurs in the Port Hacking system (Fig. 46), is probably a reflection of the poor planktonic environment available. The nutrient uptake is probably dominated by algae and fixed benthic plants, with relatively slow turnover.

If we accept bottom oxygen deficit as evidence of trophic levels (Thienemann 1928), then the minimum of 8 per cent. oxygen saturation in the bottom water at Station 5*A* in the Swan River is comparable with a figure of 5 per cent. saturation for bottom water in the Port Hacking system in March 1949. However, associated with the former oxygen deficit were 32 μg./l. of phosphates, while with the latter were 115 μg./l. of phosphates. Bearing in mind the relatively enormous phosphate discharge into the Swan River (by comparison with that into the Port Hacking system), the low level of efficiency of phosphate fixation in the waters of the former is apparent.*

TABLE 8

CHEMICAL PROPERTIES OF THE BOTTOM DEPOSITS IN THE SWAN RIVER, SEPTEMBER 1946

Station	Interstitial Phosphate (μg./g. mud)	Adsorbed Phosphate (μg./g. silt)	Total Phosphate (μg./g. silt)	Total Ferric Iron (μg./g. silt)	Organic C	Total N	C/N	Silt (%)
1	0	0	630	55.2	6	2.1	28.6	1
2	0	0	732	20.3	29	3.5	8.3	3
3	1	42	587	16.3	19	2.7	7	3
4	0	26	608	18.7	28	4.9	5.6	11
5	1	67	889	23.4	35	4.5	7.7	1
5*a*	2	90	608	20.0	40	4.1	9.8	25
6	0	59	476	7.3	25	2.6	9.6	19
7	5	61	488	26.7	33	2.9	11.4	92
8	0	52	445	26.9	35	3.5	10	40
9	0	215	792	54.1	47	3.4	14	7
11	0	7	279	23.1	14	1.0	14	4
12	0	55	348	12.8	25	2.5	10	8
13	0	0	360	14.5	28	2.5	11.2	57
14	0	0	150	17.3	4	0.5	8	28

Although insufficient data concerning bottom characteristics are available for comparison with eastern Australian conditions, the data given in Table 8 demonstrate several points of interest:

(1) There is a fluctuating increase in the adsorbed phosphate figures from a minimum at the extremes of the system to a maximum at Station 9. This is apparently correlated with the maximum for inorganic phosphates in the waters of this station (Fig. 32).

(2) A corresponding maximum in ferric iron occurs at the same station.

(3) The organic carbon content varies in a similar fashion to adsorbed phosphates, with a maximum at Station 9.

(4) The total nitrogen content varies in a rather irregular fashion from mouth to source, and in association with relatively low carbon figures in the basin zone (Stations 3, 4, and 5) develops very low C/N values in this region. This low C/N ratio appears to be a feature of most

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* The volume of water in the estuarine basins is much greater in the Swan River than in the Port Hacking system.

south-western Australian systems, although its significance is as yet not known.

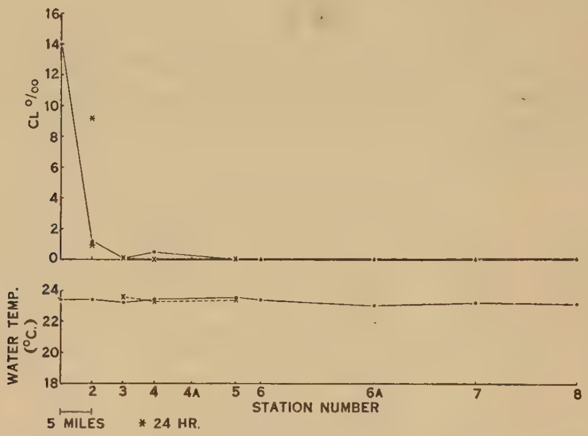

Fig. 27.—Longitudinal distribution of chlorinity and temperature in the Macleay River, January 27, 1948.

(5) The variation in silt content of these bottom muds does not conform to a zonal distribution of the type found in eastern Australian systems, but appears to be governed by the alternate effects of scouring and sedimentation rather than by electrolytic flocculation within the gradient zone.

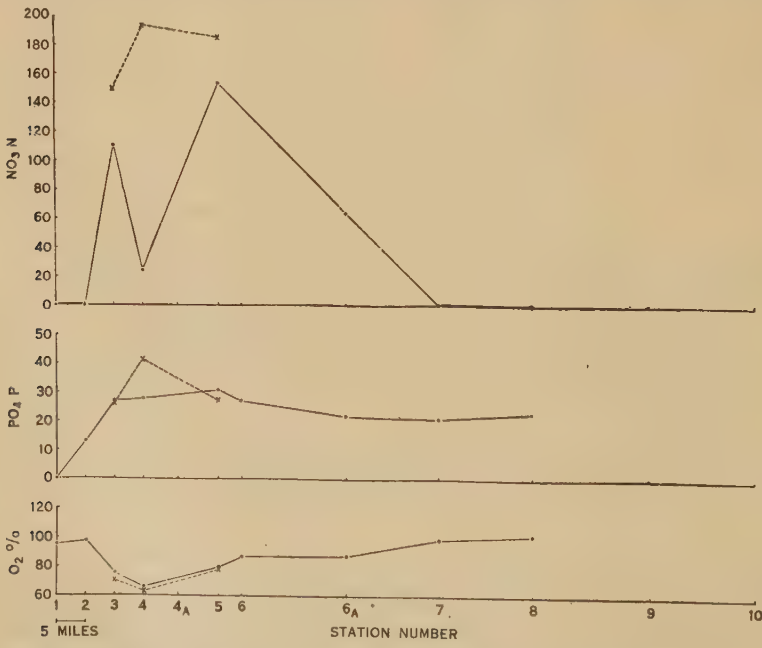

Fig. 28.—Longitudinal distribution of nitrate N, phosphate P, and O_2 percentage saturation in the Macleay River, January 27, 1948.

(*d*) *Bathymetric Features and Zonal Dominance of Some Estuarine Systems*

(i) *Methods of Calculating Water Volumes.*—Two methods have been followed in the computation of water volumes. In the first, which is termed the contour method, depth contours were plotted at intervals determined by the bathymetric features of each individual system. By means of the planimeter, the areas of successive isobathic sheets were then calculated and multiplied by the corresponding depth interval. This process was repeated over the range of isobathic sheets and the total volume obtained by summation. This method is extensively followed in the calculation of lacustrine volumes (Welch 1948) in which fairly regular slopes enable

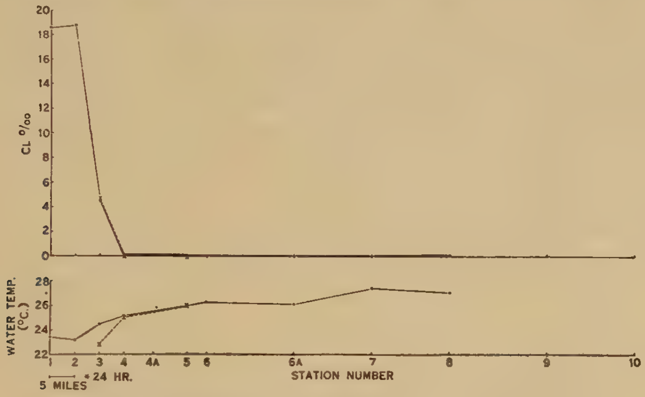

Fig. 29.—Longitudinal distribution of chlorinity and temperature in the Macleay River, March 22, 1949.

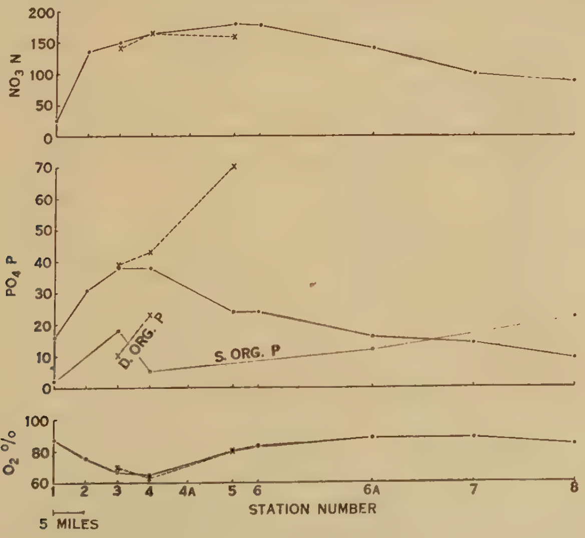

Fig. 30.—Longitudinal distribution of nitrate N, phosphate P, and O_2 percentage saturation in the Macleay River, March 22, 1949.

the location of the isobaths to be determined with some degree of confidence.

In estuarine studies it is often difficult, in view of the rapid and irregular changes in depth, to establish the course of the isobaths, and the second method is then used. In this method, which is termed the mean depth method, the surface of the estuarine system is divided into convenient areas for planimetric estimation. A mean depth in each area is then computed by arithmetical summation of all the depth values available (assuming that the latter are uniformly distributed). The mean depth is then multiplied by the surface area. Finally, the whole volume is calculated by the summation of volumes of water within each of the subareas of the estuarine system. This second method can obviously be used only when a large number of evenly distributed depth observations are available. The bathymetric data for Australian estuarine systems are for the most part useless for the computation of the total volumes of estuarine systems. In the central New South Wales systems sufficient data are available for a calculation of the volumes of some of the zones of the Port Hacking, George's River-Botany Bay, Hawkesbury River, and Port Stephens systems. In most of the other systems investigated bathymetric information is available in the vicinity of the mouth only.

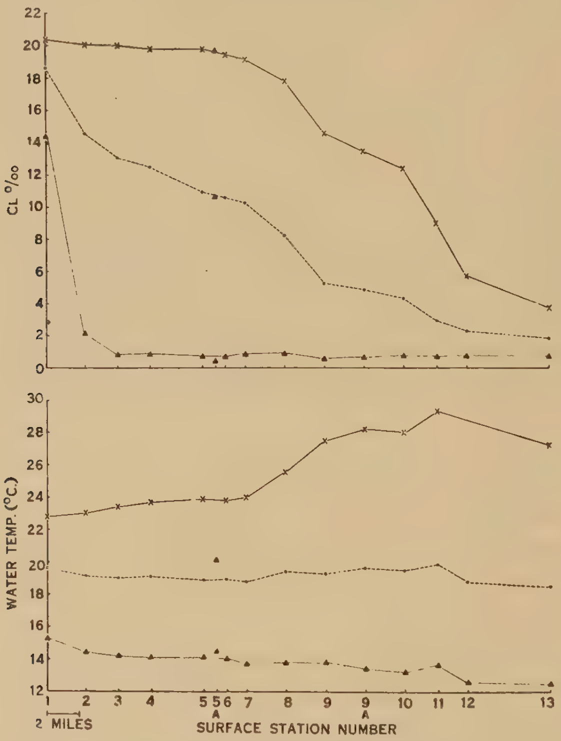

Fig. 31.—Surface mean and maximum-minimum values of chlorinity and temperature for all 1947 data in the Swan River.

(ii) *Zonal Volumes.*—In Table 9 the zonal volumes of some estuarine systems are given. Under the heading "Method of Calculation," 1 refers to the contour method and 2 to the mean depth method of calculation of water volume.

(iii) *Zonal Dominance.*—From the data in Table 9 it is clear that the marine zone in the Port Hacking system occupies by far the greatest volume of water in this system. The absence of volumes for the gradient and freshwater zones does not invalidate this conclusion. The Port Hacking system is therefore classified as marine-dominated. Because of the absence of sufficient data it is not possible to diagnose zonal dominance in the Botany Bay-George's River system with any accuracy, but it is interesting to note the low volume of the marine zone in this system. This fact, in conjunction with the considerable area of the tidal zone of this system, enables one to adopt a provisional classification of tidal zone dominance for the Botany Bay-George's River system.

In the Hawkesbury River system it is clear, in spite of the absence of the volume of the freshwater zone, that the gradient zone occupies the maximum volume. This system is therefore classified as gradient zone dominated.

TABLE 9

ZONAL VOLUMES OF SOME AUSTRALIAN ESTUARINE SYSTEMS

System	Method of Calculation	Water Volume (cubic metres x 10^{-6})			
		Marine Zone	Tidal Zone	Gradient Zone	Freshwater Zone
Pt. Hacking	1	63	7	Incomplete data	No data
Botany B-George's R.	2	37	Incomplete data	Incomplete data	No data
Hawkesbury R.	2	97	276	944	Incomplete data
Pt. Stephens	2	312	317	Incomplete data	No data

In the Port Stephens system almost equal volumes are occupied by the marine and tidal zones. This position is developed as a result of the bifurcation of the system, by a narrow connecting channel, into two basins, the outer of which is marine-dominated and the inner dominated by the shallow mud flats and associated hydrological features of the tidal zone.

It is interesting to note that in this system the greatest area of oyster farming in New South Wales is cultivated in the inner basin, while extensive spat collecting is carried out in the outer, marine-dominated basin. This system has therefore to be considered as rather unique on account of its unusual physiolographical features, and no major zonal dominance can be assigned to it.

(*e*) *Conflict Patterns in Estuarine Systems*

(i) *Conflict and Zonal Distribution of Hydrological Properties.* — As discussed and defined in Section V (*a*) (iii), the conflict in estuarine systems is independent of general circulation and mixing exchanges. It is a property peculiar to estuarine waters, and can only be developed to a maximum in the presence of a gradient zone of hydrological properties, and by reason of a diurnal tidal rise and fall of water level.

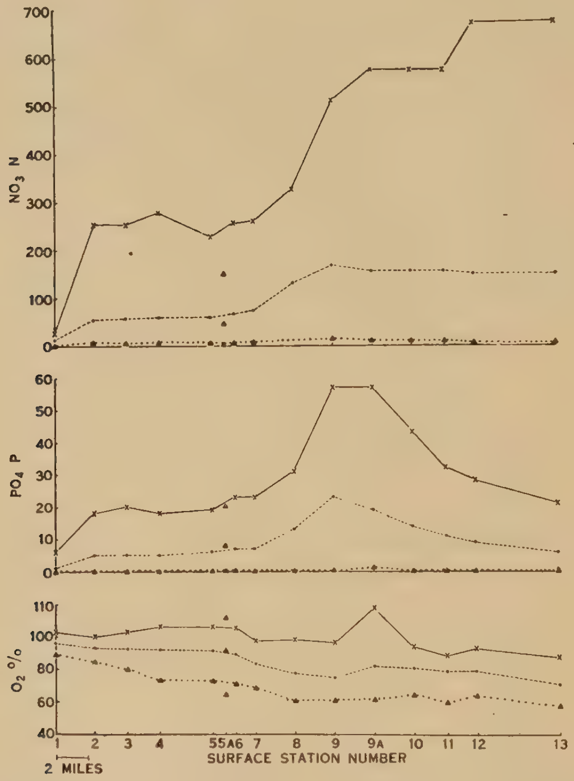

Fig. 32.—Surface mean and maximum-minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1947 data in the Swan River.

It is, of course, fundamental to suppose that in the zone of maximum spatial change in Cl°/oo, i.e., the gradient zone, any given displacement will cause the maximum variation in that property at either some fixed reference point (Fig. 35*A*), or at some fixed Cl°/oo level (Fig. 35*B*). As is demonstrated in these two figures, a constant displacement will develop a conflict proportional to the Cl°/oo gradient angle.

Although the temperature of water masses in an estuarine system is affected by a similar displacement cycle, the longitudinal variation in this property is so comparatively slight that any diurnal variation is largely caused by local insolation and heat exchanges rather than by translatory motion of water masses with different thermal properties. Normally, therefore, the diurnal cycle of water temperature follows the air temperature cycle, with some departures caused by horizontal movement of adjacent water masses.

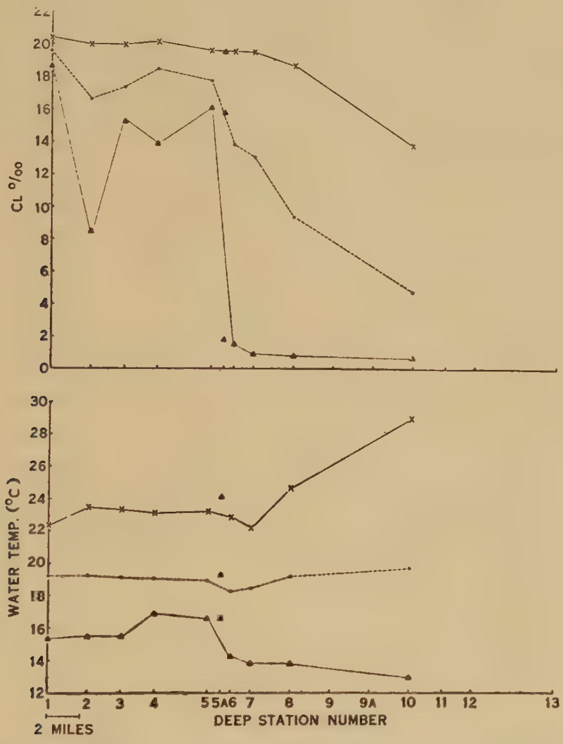

Fig. 33.—Bottom mean and maximum-minimum values of chlorinity and temperature for all 1947 data in the Swan River.

As dissolved oxygen is rather non-uniformly distributed in an estuarine system and is, moreover, influenced by biological factors subject to rather wide variation in intensity, its diurnal conflict pattern varies widely. In the marine and estuarine zones the biological factors dominate, and a characteristic photosynthetic curve, with supersaturation in dayght and undersaturation in the night period, is typical. In the gradient one the photosynthetic effect is diminished, and a regular cyclical curve orresponding to that for chlorinity is developed.

The nutrient salts are relatively uniformly distributed throughout the greater part of an estuarine system, and are also subject to biological demands that vary greatly in intensity. In general, however, the diurnal variation in nutrient salts follows a similar cyclical pattern to that of hlorinity.

(ii) *Zonal Variation in Chlorinity Conflict.*—In Figure 36 the imultaneous variation in surface chlorinity, water temperature, and tide height at a number of stations in the George's River-Botany Bay system has been plotted. For comparison, comparable data collected at similar times from Hungry Point, Port Hacking, have been included. The chlorinity data very clearly fall into three distinct categories. In the first, which includes stations within the marine and tidal zones of the system, no chlorinity conflict is developed. In the second, which includes the Picnic Point data from within the gradient zone, a regular chlorinity conflict is established. In the third, into which fall the stations worked within, or in the vicinity of, the freshwater end of the system, little or no chlorinity conflict is apparent.

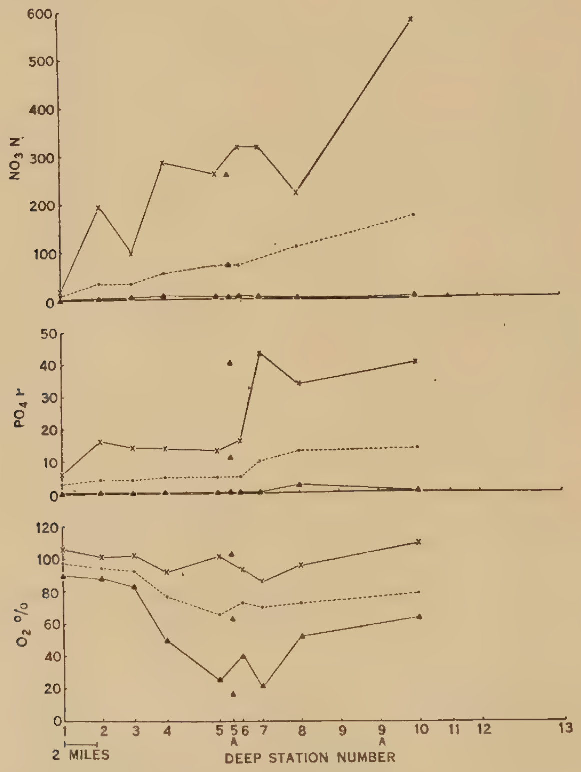

Fig. 34.—Bottom mean, maximum, and minimum values of nitrate N, phosphate P, and O_2 percentage saturation for all 1947 data in Swan River.

In Figure 37 there is plotted the simultaneous diurnal variation in surface chlorinity, water temperature, and tide at a number of stations within the Port Stephens estuarine system. The chlorinity curves fall into two distinct categories. In the first, into which fall chlorinity data from the stations at Pipeclay Creek, Tillingherry Creek, and Pindimar within the estuarine zone of the system, the chlorinity conflict is only slight, although the mean chlorinity varies from locality to locality. In the second, into which data from the Tea Gardens station, situated within the gradient zone of the Myall River, can be placed, a pronounced chlorinity conflict is developed. At this juncture it is interesting to make the ecological note that whilst oyster cultivation is successfully carried out at the station falling within the first category, no successful cultivation has been carried out in recent years at Tea Gardens.

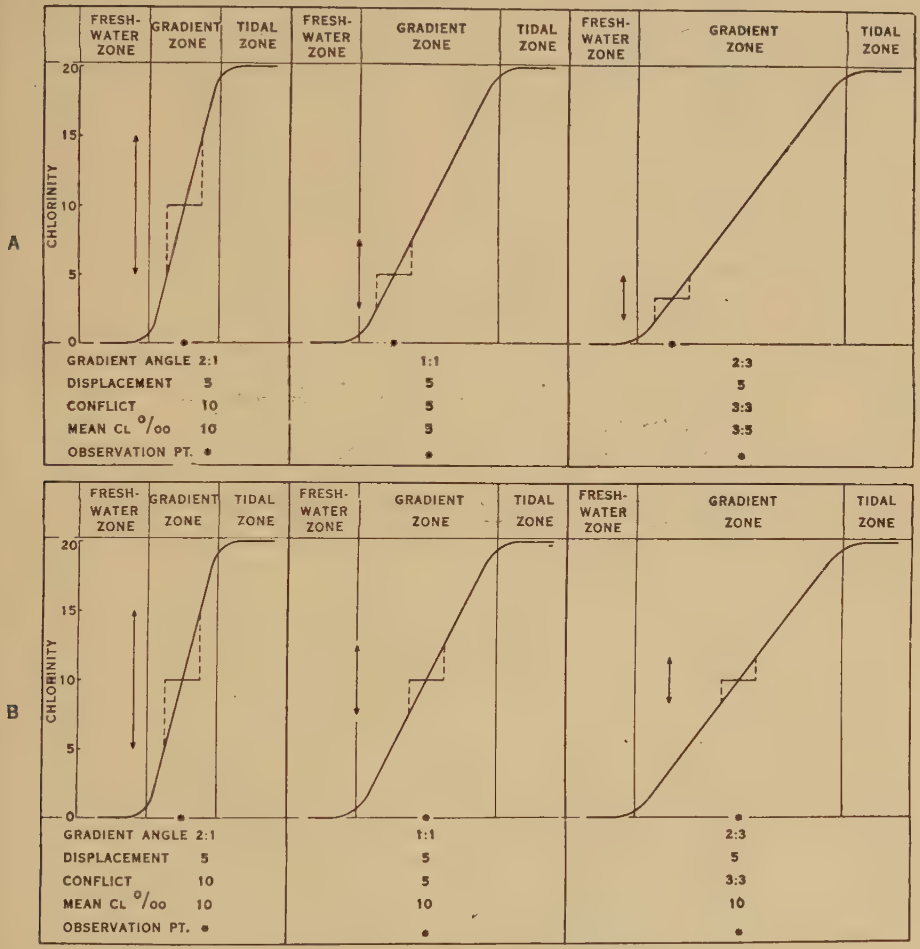

Fig. 35.—Variation in chlorinity conflict caused by different Cl°/oo gradient angles, and location of observation points, within an estuarine system.

Figure 38 depicts the simultaneous surface and bottom variation in chlorinity at a number of stations within the Port Hacking system. At the Audley and upper South-West Arm stations, within the gradient zone of the Port Hacking River and South-West Arm tributary, a distinct chlorinity conflict was developed in surface waters, and although the bottom observations were made in waters with depths not exceeding about 3 fathoms, practically no bottom chlorinity conflicts were developed at these stations. The almost complete absence of a chlorinity conflict is clearly demonstrated at the South-West Arm and Lillipilli stations located near the marine end of the Port Hacking system.

It is apparent, therefore, that within an estuarine system whose hydrological properties are zoned as in Figure 6, the chlorinity conflict, and to a lesser degree conflict of other hydrological properties, are at a maximum in the gradient zone, at a minimum in the tidal and marine zones, and by definition absent in the atidal freshwater zone.

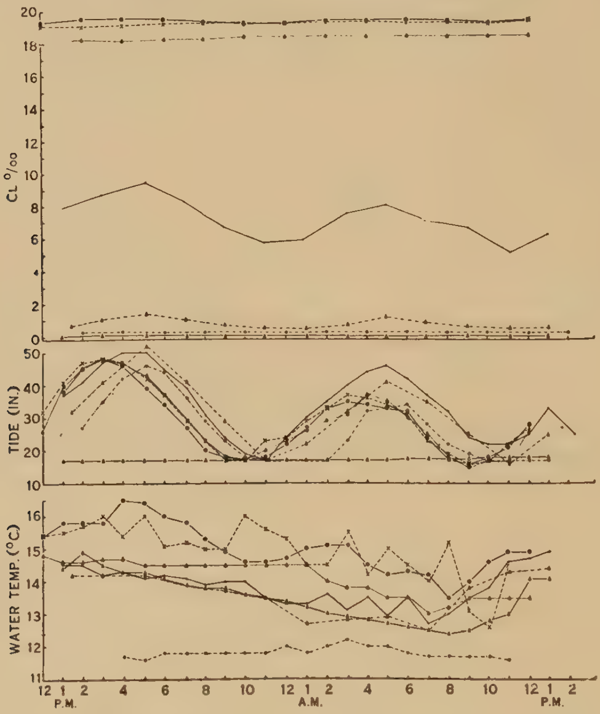

Fig. 36.—Simultaneous diurnal variation in surface chlorinity, water temperature, and tide at the following localities in George's River and Botany Bay, 17.viii.1945:

● — ● Port Hacking, Hungry Point.
●—● Picnic Point.
△ - · - △ Hollywood.
× - - × Kurnell.
● - · - ● Prospect Creek.
▲ · · ▲ Shell Point.
△ — △ Ingleburn.

(iii) *Depth Variation of Chlorinity Conflict.*—In the cellular circulating system of eastern Australia (Section IV (*c*)), little difference in conflict behaviour of surface and bottom waters is normally encountered. Figure 39, showing conflict data off Nelson's Bay, Port Stephens, and Figure 40, showing conflict data in South-West Arm, Port Hacking, are illustrative in this regard. If, however, the cellular circulation is disrupted and stratification develops, a considerable divergence can ensue between surface and bottom conflict values. For example, at upper South-West

Arm in May 1939 (Fig. 38), an oscillation of the surface-diluted water mass developed an appreciable Cl°/oo conflict, although the bottom waters were largely unaffected.

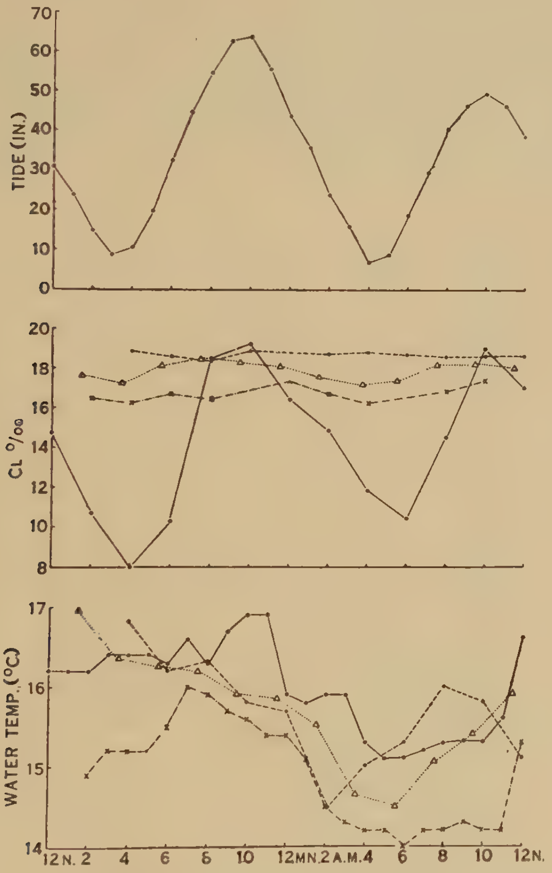

Fig. 37.—Simultaneous diurnal variation in surface chlorinity, water temperature, and tide at the following localities in Port Stephens in August 1942:
△ . . △ Tilligherry Creek. × — × Pipeclay Creek.
● — ● Tea Gardens. O - - O Pindimar.

(iv) *Chlorinity Conflict in Atidal Estuarine Systems.*—In the south-western Australian area astronomical tides are rather weakly developed, and random wind-generated vertical movements of the coastal waters occur (British Admiralty 1934). Hence, by definition, a conflict such as occurs in eastern Australian systems cannot be developed. Normally, therefore, little diurnal variation at any reference point within these systems occurs. During floods, when stratification has developed and there is a persistent seaward movement of fresh water in the surface layers, a diurnal variation in Cl°/oo of some magnitude is often encountered.

In Figure 41, there are plotted the surface and bottom diurnal variations in hydrological properties of the waters at Fremantle Railway Bridge. In spite of the relatively shallow depth of less than 7 metres, the almost complete absence of a Cl°/oo conflict in the bottom waters is evidence of their relative isolation. At the surface a diurnal variation of some considerable magnitude in chlorinity and temperature can be detected. In the absence of tidal rise and fall, this diurnal variation is considered to be caused by changes in the marine and freshwater isostatic pressures under the influence of wind and other meteorological factors.

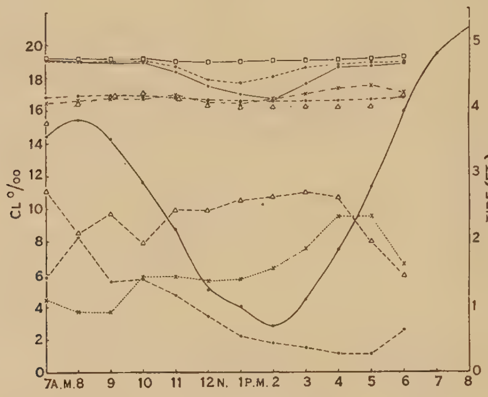

Fig. 38.—Simultaneous diurnal variation in surface chlorinity and tide at the following localities in Port Hacking in May 1939:

● - - ● Audley Weir Surface.
● - · - ● Audley Weir Deep.
× . . . × Audley Wall Surface.
× - ·· - × Audley Wall Deep.
△ - - △ Head South-West Arm Surface.
△ . . △ Head South-West Arm Deep.
○ - - ○ Mouth South-West Arm Surface
○ — ○ Mouth South-West Arm Deep.
□ — □ Lillipilli Point Surface.

(v) *Chlorinity Conflicts in the Tamar River, Tasmania.*—In Figures 42 and 43 are depicted the diurnal variations in hydrological properties at stations within the gradient zone of the Tamar River. In Figure 42, the conflict under winter flood conditions has been plotted. In spite of a big rise and fall of tide, practically no chlorinity conflict was developed. In Figure 43, the conflict under summer drought conditions has been plotted. Again, in spite of a large rise and fall of tide, no chlorinity conflict has been developed. This anomalous behaviour is probably due to the absence in the gradient zone of this system of any large translatory movement of water, although there takes place a tremendous backing up of the waters, as is revealed by the rise and fall of water level. A rise and fall of water level need not, therefore, of necessity lead to the development of a conflict.

(vi) *Chlorinity Conflicts in Freshwater-Dominated Systems.*—Figure 44 depicts the diurnal variation in hydrological properties at a station near the mouth of the Macleay River, N.S.W. The relatively enormous chlorinity conflict is developed in spite of a small rise and fall of tide. This phenomenon is caused chiefly by the steepness of the chlorinity gradient zone (Figs. 27 and 29), which enables a big conflict to develop with relatively little horizontal displacement.

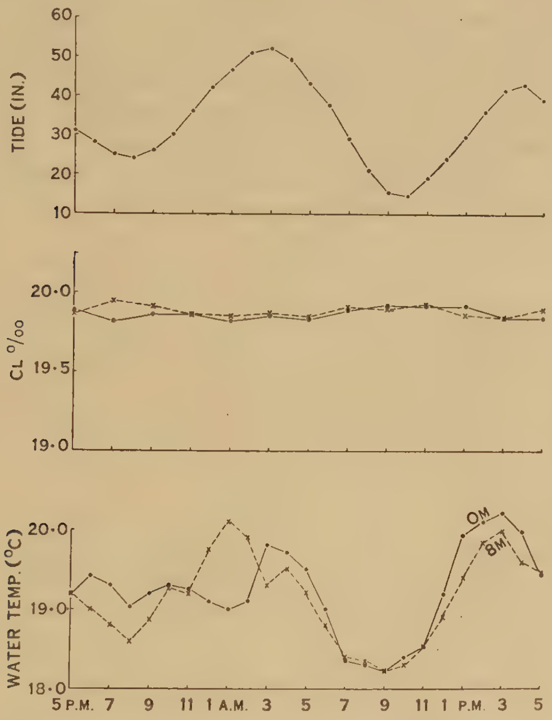

Fig. 39.—Diurnal variation in surface and bottom chlorinity, water temperature, and tide, off Nelson's Bay, Port Stephens, 12-13.v.1943. Water depth, 10 metres.

The examples chosen to illustrate this section demonstrate that some degree of hydrological conflict, and especially chlorinity conflict, is developed in all estuarine systems. The maximum development of this chlorinity conflict is generally found within the surface layers, and is associated with the gradient zone of the system. In some systems with a normal tidal rise and fall of water level, the chlorinity conflict is almost absent. In certain systems without cyclical tidal movement the sudden changes in hydrological properties can be compared with those classified as conflicts in normal tidal controlled systems. These atidal conflicts are probably more severe in ecological effects than the normal conflict patterns of eastern Australian systems. A flow diagram giving the relationship between the various factors responsible for conflict development is given in Figure 6.

VI. Productivity of Estuarine Systems

(*a*) *Productivity of Estuarine Waters*

(i) *Definition of Productivity.*—Marine productivity in basic units is defined as the annual rate of production of protoplasm per unit volume (Sverdrup, Johnson, and Fleming 1942). In so far as it is difficult to estimate the total protoplasmic content of a water mass, the relative productivity is often estimated. The relative productivity is defined as the unit volume production of phytoplankton, determined often in terms of Harvey's chlorophyll units (1934). The productivity of the zooplankton and the larger marine organisms is linked closely with the availability of phytoplankton, and the relative productivity is therefore a fairly convenient measure of total plankton productivity.

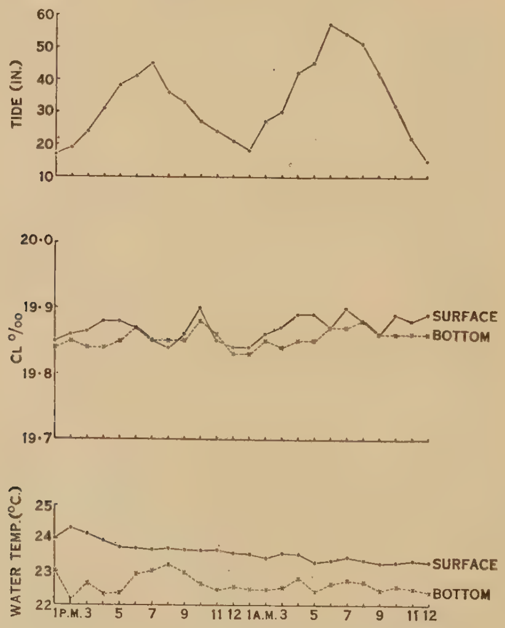

Fig. 40.—Diurnal variation in surface and bottom chlorinity, water temperature, and tide in South-West Arm, Port Hacking, 17-18.iii.1943. Water depth, 15 metres.

Phytoplankton productivity is dependent upon the availability under proper light, temperature, and turbulence conditions of certain nutrients and, in particular, phosphates (Riley 1946; Clarke 1946). In the absence of direct plankton estimates of productivity and their possible minor role (Section VIII) in Australian estuarine waters, there has been developed a method of assessment based upon the annual cycle undergone by various forms of phosphates. This method is discussed in Section VI (*a*) (v).

(ii) *Flood Cycles and Estuarine Productivity.*—As demonstrated in Section V (*a*) (i), the estuarine systems of Australia can be divided into three groups on the basis of flood characteristics. In the first group can be placed those estuarine systems in which the annual flood cycle invariably occurs during the summer months. The maximum of marine domination occurs in these systems during the winter-spring period. Plankton cycles of the neritic pattern such as occur in the Port Hacking system (Section VI (*a*) (iii)) should therefore be favoured by the summer flood nutrient replenishment prevailing in this group of systems. However, in the northern New South Wales estuarine systems, freshwater domination is sufficient even during the winter-spring periods (Fig. 27) to exclude any appreciable marine influx. Production in these systems, therefore, falls short of the potential level (Section VI (*a*) (v)). If, on the other hand, these northern New South Wales systems could have their nutrient stocks replenished by summer flooding, with rapid post-flood development of a substantial marine zone, then plankton fixation of nutrients and turnover

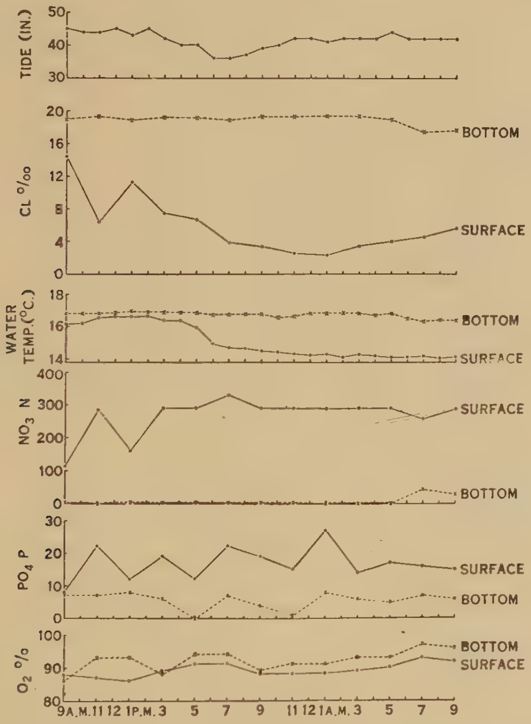

Fig. 41.—Diurnal variation in surface and bottom hydrological properties at the Fremantle Railway Bridge, Swan River, 23-24.vii.1947.

should be very high during the ensuing winter and following spring.

In the second group are placed those systems in which the annual flood cycle invariably occurs during the winter-spring period. Maximum development of marine influences in such systems occurs during the summer period. Vernal plankton production bursts are impossible in these systems, and the post-flood summer fixation and turnover of nutrients is rather low. The Swan River system is a typical member of the group (Fig. 54).

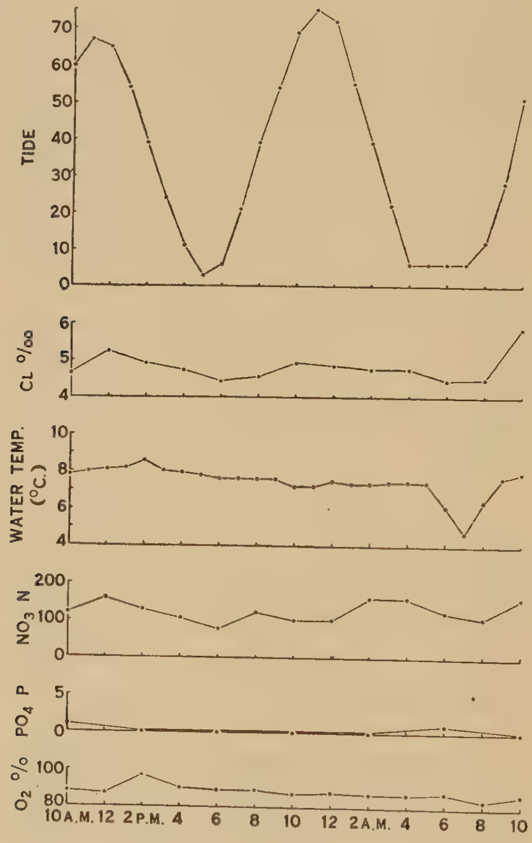

Fig. 42.—Diurnal variation in surface hydrological properties off Deviot, Tamar River, 1-2.vii.1947.

In the third group are placed those systems with no regular annual flood cycle, but with the annual discharge spread over a considerable number of minor floodings. In these systems the circulation pattern (Section IV (*c*)) is often able to absorb practically all of these minor flood discharges without appreciable displacement of the hydrological zones. The Hawkesbury River is a typical example of the type (Fig. 47). The nutrient level of these systems is, however, generally low, and probably acts as a major limiting factor in their plankton productivity. The possibility that productivity at the bottom mud surface plays an important role in the overall productivity of such systems (Section VI (*b*) (iii)) must be considered. The relative stability of these systems permits of the development of intense local nutrient turnover of the Port Hacking type (Section VI (*a*) (iii)) in the deep waters of the sheltered bays and inlets adjacent to the mouth.

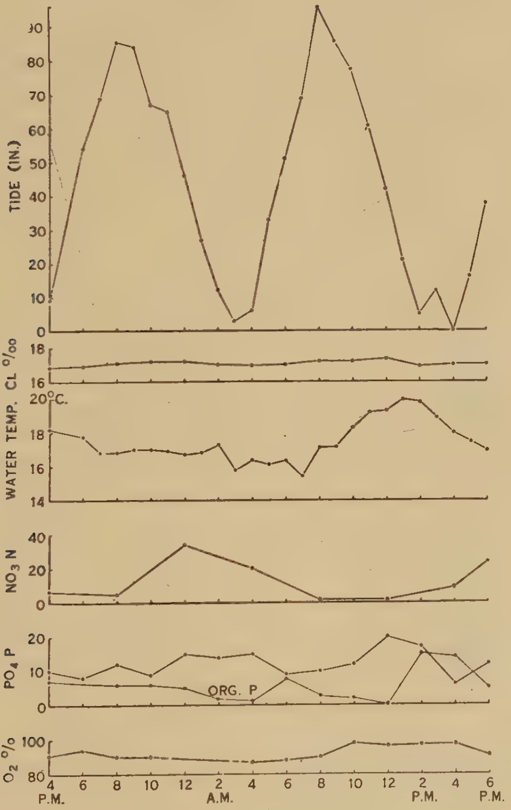

Fig. 43.—Diurnal variation in surface hydrological properties off Deviot, Tamar River, 5-6.iii.1948.

(iii) *Seasonal Cycles of Nutrients in Estuarine Waters.*—In the marine zone of the central eastern Australian estuarine system, a seasonal cycle of nutrients possessing the following features is characteristic:

(1) Commencing in spring and extending into late summer there occurs in bottom, and to some extent in surface waters, a continuous series of inorganic phosphate maxima at fairly regular intervals (Fig. 46).

(2) Alternating with these peaks, although with some overlapping, occur maxima of organic phosphates.

(3) Associated with the inorganic phosphate maxima are minima of dissolved oxygen (Fig. 45) and hydrogen ion concentration (Fig. 58).

(4) A corresponding cycle of nitrate nitrogen is not in evidence (Fig. 46).

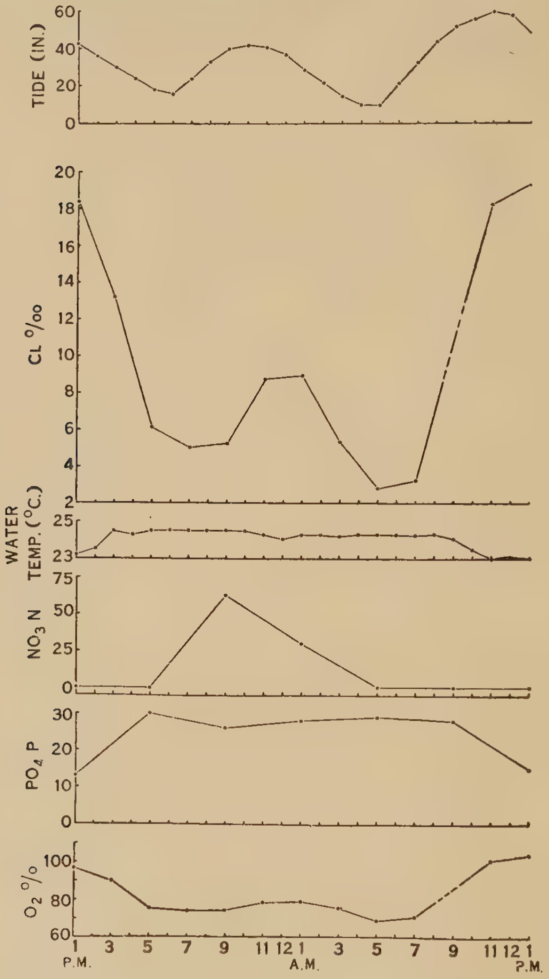

Fig. 44.—Diurnal variation in surface hydrological properties off Jerseyville, Macleay River, 27-28.i.1948.

(5) These phosphate cycles are not associated with chlorinity fluctuations and presumably are, therefore, an effect of local turnover.

This phosphate cycle is particularly well developed in the deep basins of the Port Hacking system, but corresponding cycles on a reduced scale are apparent in the Hawkesbury River (Fig. 48). Scatter diagrams of the inorganic phosphate to dissolved oxygen relationship for Station 4, Port Hacking (Fig. 49), for Station 1, Botany Bay (Fig. 50), and for Station 7, George's River (Fig. 51), demonstrate the general existence of this turnover in central New South Wales systems.

In the freshwater-dominated northern New South Wales systems, the data available do not show any local turnover of phosphates in the marine end of the system (Fig. 53). Similarly, in the Swan River system, the flood peaks of phosphates are clearly associated with flood cycles and are not followed by any local turnover in the post-flood period (Figs. 54 and 55).

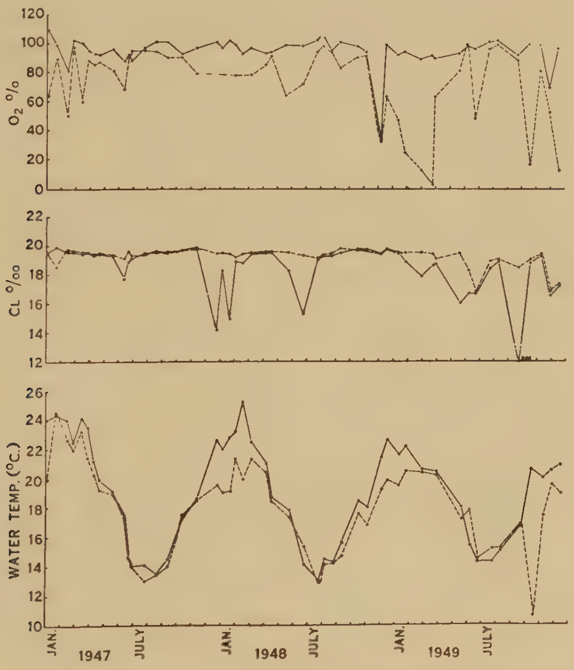

Fig. 45.—Seasonal cycles of chlorinity, water temperature, and O_2 percentage saturation at Station 4, Port Hacking, 1947-49.

●—● Surface data. ●--● Bottom data.

In the D'Entrecasteaux Channel, Tasmania, associated with the Derwent estuarine system, a slow persistent turnover of phosphates, with alternating peaks of inorganic and organic forms, seems to be characteristic of these colder semi-neritic waters (Fig. 56). Again, there does not appear to be any corresponding cycle of nitrate nitrogen.

In general, therefore, the marine or lower tidal zone of Australian estuarine systems exhibits a good deal of latitudinal variation in the development of this phosphate cycle. There is present an intense spring-summer turnover of phosphates in the central New South Wales systems, a persistent, almost annual turnover on a reduced scale in the southern

Tasmanian systems, but an absence of such a turnover in the freshwater-dominated northern New South Wales and the atidal south-western Australian systems. In all systems, however, no corresponding cycle of nitrate nitrogen can be detected. It is probable, as has been suggested in Section V (*a*) (iv) (1), that nitrogen is assimilated at a lower level, probably as ammonium nitrogen in the nitrogen cycle.

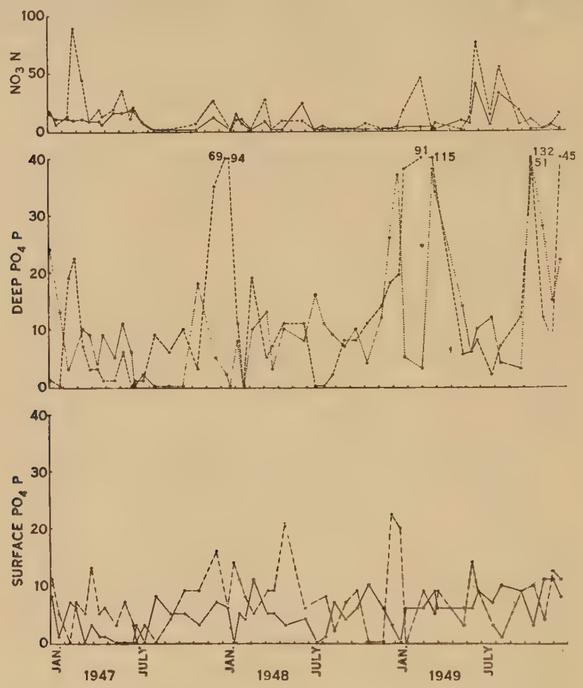

Fig. 46.—The seasonal cycles of nitrate N, and phosphate P at Station 4, Port Hacking, 1947-49.

Nitrate N

● — ● Surface data. ● - - ● Bottom data.

Phosphate P

● — ● Surface inorganic P. ● - - ● Bottom inorganic P.
● - · - ● Surface organic P. ● . . . ● Bottom organic P.

Harvey (1940) has shown in culture experiments the preference of phytoplankton for ammonium rather than nitrate sources of nitrogen, and this may provide an explanation for this anomaly. It may be, however, that the environmental factors do not favour the development of the necessary bacteria for the conversion of ammonium to nitrate nitrogen. Certainly, relatively large quantities of nitrate nitrogen are discharged into each system by run-off discharge (Figs. 19, 24, 30, 32), and are practically always present in the freshwater and lower gradient zones. Hence it would appear as if nitrate nitrogen cannot be classed as a limiting factor controlling productivity levels within the marine zone of these systems. Presumably, therefore, in the central New South Wales systems, inorganic phosphate is the more important of these two trace elements when they are considered as limiting factors in water productivity.

During 1949, using the method outlined in Section III (*a*), a separation of the Port Hacking total organic phosphates was made into soluble and particulate fractions. In Figure 57 the annual cycles of both these forms of organic phosphate at Stations 1 and 4 have been plotted. As shown by the density and direction of the arrows in the upper portion of the figure, there was considerable movement of foreign diluted water masses into the region of these two stations during the year, and it is not possible, therefore, to accept the results as typical of a more normal year or as being entirely developed by an *in situ* turnover.

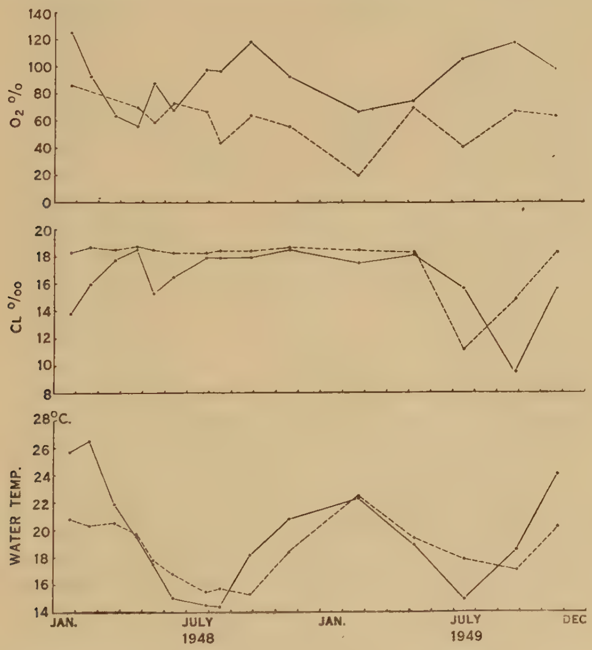

Fig. 47.—Seasonal cycles of chlorinity, water temperature, and O_2 percentage saturation at Station 3, Hawkesbury River, 1948-49.
● — ● Surface data. ● - - ● Bottom data.

It is evident, however, that the organic phosphate cycles at these two stations are comparable in magnitude in the surface waters, but that the marked summer and spring peaks in both soluble and particulate organic phosphates in bottom waters occur only at Station 4. At this station, the particulate organic phosphates were at a peak in December 1948, March 1949, and October 1949. The soluble organic phosphates displayed maxima in January 1949 and January 1950. Whether these maxima can be associated with the previous particulate organic phosphate peak is questionable, but hardly likely. From the October peak in the latter form to the succeeding soluble organic phosphate peak in January 1950 is a period of some two and a half months, which hardly seems requisite in the light of laboratory data on the speed of such transformations. It is more probable that the transformation of particulate into soluble organic and thence into inorganic phosphates has been completed in many cases in between surveys of the system and will not, therefore, be revealed in the data.

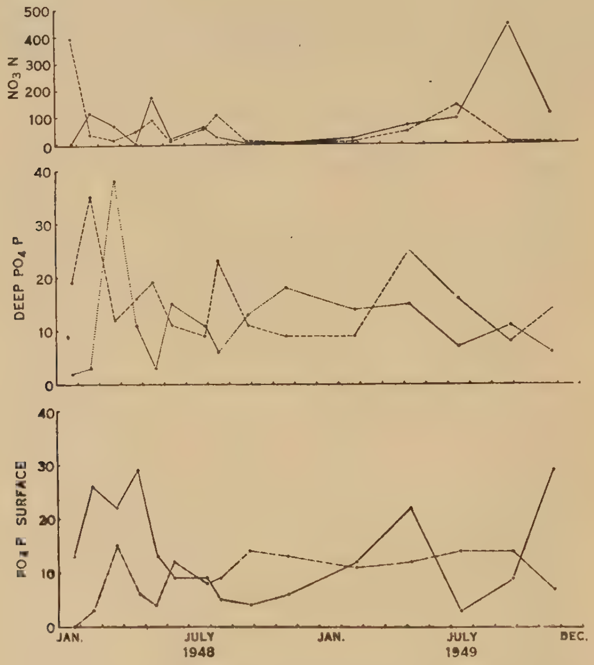

Fig. 48.—Seasonal cycles of nitrate N and phosphate P at Station 3, Hawkesbury River, 1948-49.

Nitrate N

● — ● Surface data. ● - - ● Bottom data.

Phosphate P

● — ● Surface inorganic P. ● - - ● Bottom inorganic P.
● - · - ● Surface organic P. ● . . ● Bottom organic P.

The Port Hacking system affords an excellent opportunity for the study of a phosphorus cycle under somewhat magnified conditions, compared with that occurring in the open sea. Moreover, because of the semi-isolation of the bottom waters, this cycle almost possesses the characteristics of an *in situ* turnover. In future years, therefore, an endeavour will be made to carry out more frequent sampling and detailed analyses of the waters of this system in an endeavour to obtain more fundamental data on this cycle.

(iv) *The Cycle of Inorganic Phosphates in the Bottom Waters of the Central New South Wales Estuarine Systems.*—As demonstrated in Section VI (*a*) (iii), a cycle of inorganic phosphates, associated with similar cycles of dissolved oxygen and pH, is encountered in the bottom waters of New South Wales estuarine systems during the spring-summer period. In the deep basin of the Port Hacking system at Station 4, in which there is an average depth of about 25 metres, a more detailed analysis of these cycles can provide some clues as to their origin.

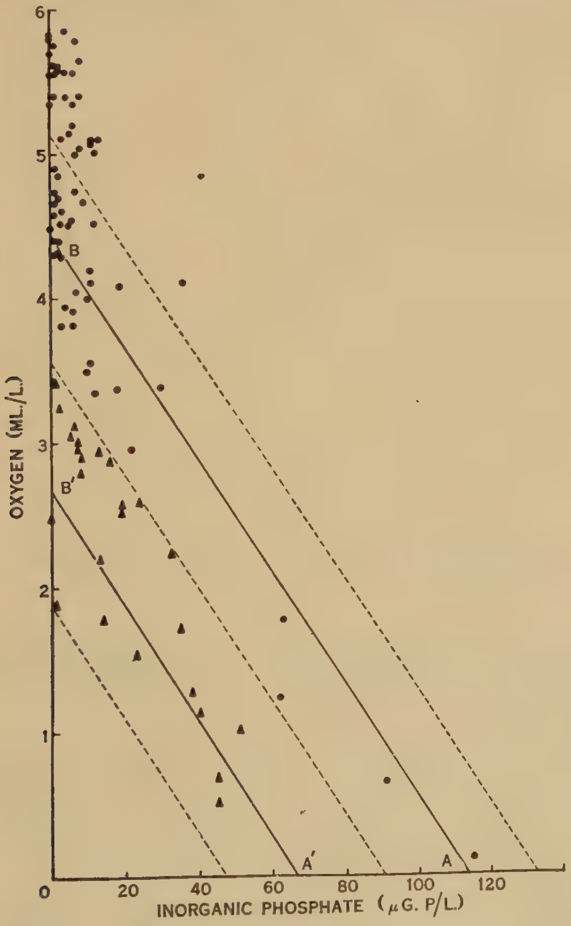

Fig. 49.—Relationship between inorganic phosphate and dissolved oxygen in the bottom waters of Station 4, Port Hacking.

If a scatter diagram of the relationship between dissolved oxygen and inorganic phosphates (Fig. 49) be examined, the spread of the data suggests either that no direct single regression of dissolved oxygen or inorganic phosphates is possible, or that a cycle of interaction between these two variables renders a preliminary grouping of the data necessary.

The second possibility has been accepted, and in Figure 49 the data have been divided into two groups and plotted with different symbols. Those plotted with dots are associated with the regression line AB, and its envelope is indicated by the adjoining dashed lines. Those plotted with triangles are associated with the regression line A′B′, the envelope of which is similarly indicated.

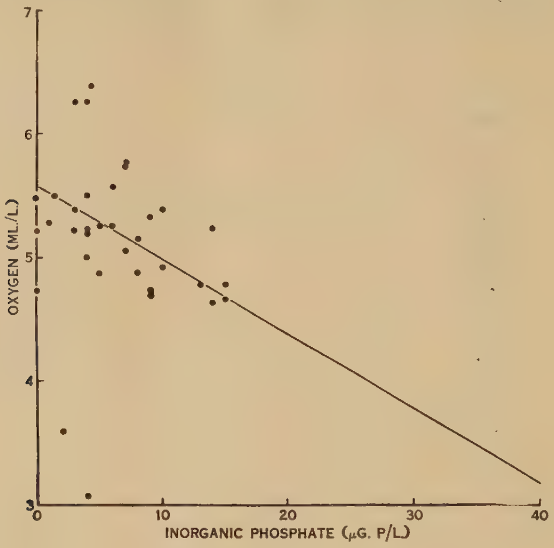

Fig. 50.—Relationship between the inorganic phosphate and dissolved oxygen content of the bottom waters at Station 1, Botany Bay.

In Figure 58 a scatter diagram of the relationship between dissolved oxygen and hydrogen ion concentrations in the bottom waters of Station 4, Port Hacking, is given. In accordance with the theory underlying the grouping of the data in Figure 49, two regression lines AB and A′B′ have been drawn through the rather limited number of observations as yet available. It is suggested that the grouping of the data into the two sections AB and A′B′ in Figures 49 and 58 can be justified by the following hypothesis:

The line AB is presumed to represent the liberation cycle in which organic degradation, utilizing dissolved oxygen of the water, liberates inorganic phosphates and carbon dioxide. The line A′B′ is considered to represent the utilization cycle, in which inorganic phosphates are synthesized into protoplasm, and equivalent amounts of oxygen are liberated during carbon fixation by photosynthesis. The divergence AA between the two cycles is considered to be due to inefficiencies in the cycle, and to losses of phosphate to the bottom muds and exchanges due to mixing with adjoining water masses. The ultimate oxygen level B′, developed by complete utilization of inorganic phosphates, is therefore below the original saturation values at B, and must return to this value by mixing exchange with the surface waters.

It is possible, of course, that cycle A′B′ may represent the liberation and AB the utilization cycle, with AA as a desorption contribution of phosphates from the mud surface. The difficulty in accepting this interpretation is the subsaturation level B′ at which the liberation cycle commences. It may be necessary, of course, for some oxygen to be utilized in organic degradation prior to phosphate liberation, but only further and more intensive study of these waters will provide an answer to this problem.

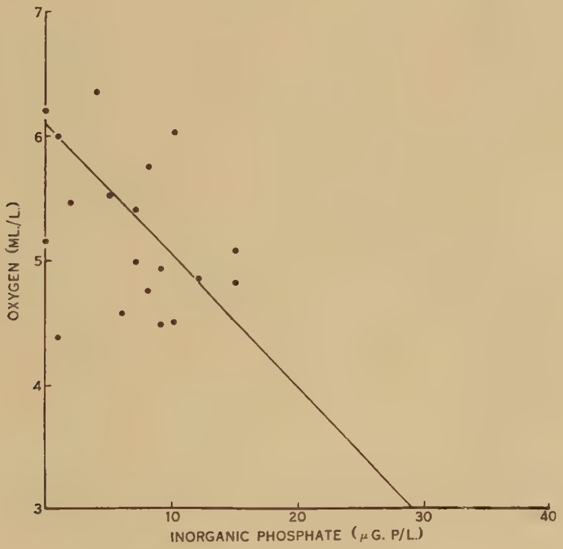

Fig. 51.—Relationship between inorganic phosphates and dissolved oxygen in the waters at Shell Point, George's River.

If we assume that the regression lines in Figures 49 and 58 have factual meaning, then it is evident that during the cycle the consumption of 1 ml. of dissolved oxygen liberates 24.4 μg. of inorganic phosphate and produces sufficient CO_2 by oxidation to lower the pH by 0.1 units. From data by Sverdrup, Johnson, and Fleming (1942), a lowering of 0.1 pH units is the equivalent of 672 μg. organic carbon oxidized to carbon dioxide. Hence the biological material decomposed during this cycle must have had a protoplasmic carbon to phosphorus ratio of 27.5 : 1. According to tables published by Fleming and quoted in Sverdrup, Johnson, and Fleming (1942), the carbon : phosphorus ratio varies from 53.2 for zooplankton down to 42 for phytoplankton. It is evident, therefore, either that the relationship deduced from the Port Hacking data is grossly in error, or that some biological material with a higher relative phosphorus content is responsible.

There is some evidence of the association of oyster spawning cycles with these phosphate peaks (data in possession of Division of Fisheries, C.S.I.R.O.) and perhaps the anomaly in the carbon : phosphorus ratio is due to the death and autolysis of oyster larvae and young spat. It is evident, too, that at the depth of water existing in the Port Hacking basin, some mixing between surface and bottom waters must have occurred.

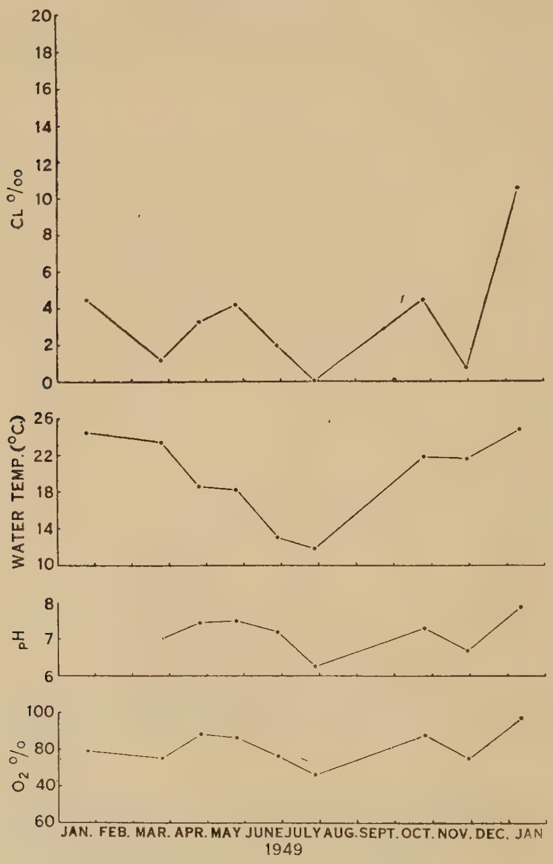

Fig. 52.—Seasonal cycles of chlorinity, water temperature, O_2 percentage saturation, and pH at Station 2, Macleay River, 1949.

If we enter regression lines on the data plotted as scatter diagrams in Figures 49, 50, and 51, calculate the amount of phosphate liberated per ml. dissolved oxygen, and then plot the phosphate figure so obtained against depth of water at that station, a linear relationship is found (Fig. 59). It is apparent from this figure that the greater the depth of water, the more phosphates are liberated per unit of dissolved oxygen. Conversely, therefore, relatively less oxygen is utilized in the liberation of a unit of phosphate at greater depths of water. This anomaly is presumably developed as the result of the water mass in question mixing with surface waters.

In view of the positive gradient of phosphates and negative downward gradient of oxygen prevailing during the part of the cycle most affected by vertical exchanges, it appears probable that the dissolved oxygen content is more influenced by such vertical transfer than is the phosphate content. On the evidence, therefore, it appears most probable that organisms richer in phosphorus than marine phytoplankton are responsible for the periodic peaks of inorganic phosphates in the bottom waters of the marine zone of central New South Wales estuarine systems.

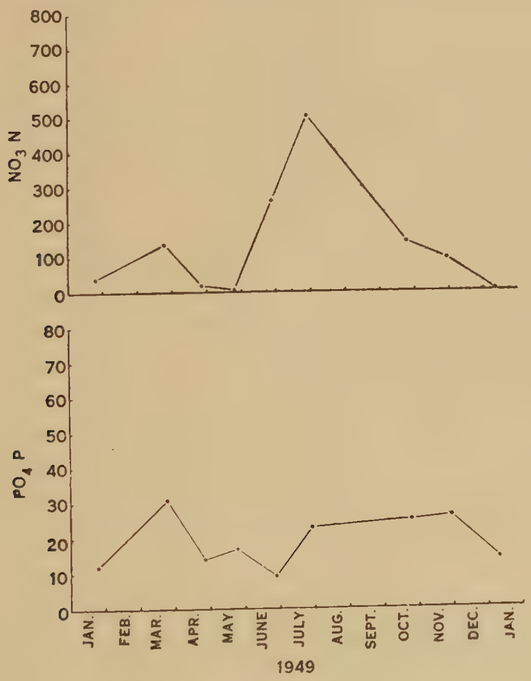

Fig. 53.—Seasonal cycles of nitrate N and phosphate P at Station 2, Macleay River, 1949.

(v) *Assessment of Productivity of a Water Mass in Terms of Inorganic and Organic Phosphate Levels.*—Laboratory tests have shown that the liberation of inorganic phosphates from plankton detritus is particularly rapid (Cooper 1935). Moreover, Armstrong and Harvey (1950) have found that the total phosphate content of a water mass is fairly constant and can be used as an identifying property. Presumably, therefore, the relative proportion of organic phosphates in a water mass during its plankton productive period is largely determined by biological activity. In the absence or lessening of such biological synthesis of organic from inorganic phosphate material, the relative proportion of organic phosphates decreases. Of course, both internal and external factors modify the effectiveness of this biological synthesis but, as a working hypothesis for critical examination, it is suggested that the ratio of organic to inorganic phosphates could provide an index of the efficiency of biological synthesis in a particular water mass. If, therefore, the total phosphate content of a water mass is unaffected by exchanges with neighbouring water masses, and if the direct planktonic uptake of organic phosphates is negligible (Chu 1946), then the diagram in Figure 60 summarizes the phosphate cycle in sea-water and the principal factors responsible for reaction rates.

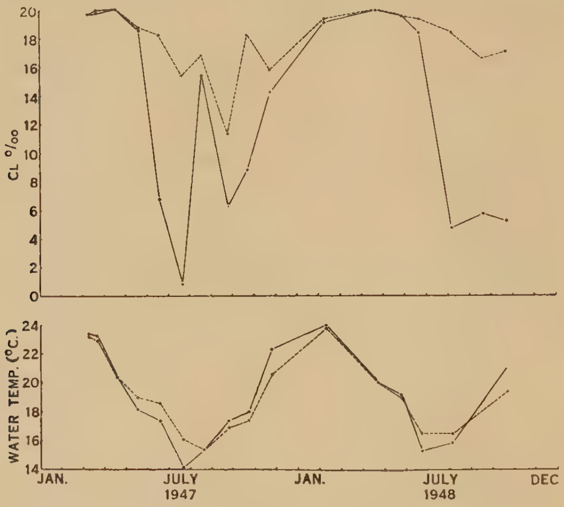

Fig. 54.—Seasonal cycles of chlorinity and water temperature at Station 3, Swan River, 1947-48.
●—● Surface data. ●- - ● Bottom data.

In an estuarine system, the waters of the marine zone, whilst affected by exchange of phosphatic nutrients with neighbouring zones and with the bottom muds of the marine zone, are apparently sufficiently isolated to develop local *in situ* turnover of nutrients (previous section).

The ratio of organic to inorganic forms of phosphates is an index of the effectiveness of the biological synthesis cycle ABC. Assuming that other external and internal factors are constant, the potential level of organic phosphates is determined by the level of inorganic phosphates and the efficiency of the cycle AC. If these assumptions be permitted, the relative productivity of a water mass can be estimated in arbitrary units by multiplying the ratio of organic to inorganic phosphates by the inorganic phosphates in the water mass.

In Table 10 are given the mean ratios of all marine zone values of organic and inorganic phosphates in eastern Australian estuarine systems. The value of each ratio multiplied by the mean inorganic phosphate figure is given in the final column and expressed as the relative productivity value. If we plot the relative surface productivity values against the latitude of the estuarine system from which it has been derived (Fig. 61) an approximation to a linear inverse relationship, with one anomaly in the case of the Macleay River value, seems apparent. It is probable, therefore, that some physical factors such as light or mean temperature (see Section V (*a*) (iv)), which vary in a progressive fashion with latitude, are dominants in the determination of these relative productivity levels. The regularity of this decrease in relative productivity lends support to this method of productivity estimation, but it is evident that considerably more information about the factors responsible for nutrient cycles must be obtained before a full appraisal of it can be made.

TABLE 10

MEANS OF AVAILABLE INORGANIC AND ORGANIC PHOSPHATE FIGURES FOR SELECTED ESTUARINE SYSTEMS AT STATIONS WITHIN THE MARINE END OF THE SYSTEM, CORRESPONDING ORGANIC: INORGANIC PHOSPHATE RATIOS, AND ESTIMATES OF RELATIVE PRODUCTIVITIES

System	Station	Depth	No. of Obs.	Mean Inorganic P	No. of Obs. for Organic P	Mean Organic P	Organic: Inorganic P	Relative Productivity
Richmond R.	Burn's Pt.	S	4	30	4	13	0.43	12.9
Macleay R.	S.W. Rocks	S	11	11	8	6	0.55	6.1
Pt. Stephens	Nelson's Bay	S	20	6	19	9	1.5	9.0
Hawkesbury R.	3	S	15	14	15	9	0.64	9.0
		D	15	16	15	12	0.75	12.0
Botany Bay	1	S	19	5	18	9	1.80	9.0
		D	19	8	17	6	1.75	14.0
George's R.	Shell Pt.	S	24	6	23	10	1.67	10.0
Pt. Hacking	4	S	32	6	31	8	1.3	7.8
		D	32	22	32	16	0.73	16.0
Tamar R.	Kelso	S	4	8	3	6	0.75	6.0
Derwent R.	Gordon	S	24	8	22	5	0.65	5.2
		D	24	8	22	6	0.75	6.0
			Mean	10.5		8.4	0.80	

(*b*) *Productivity of Estuarine Bottom Deposits*

(i) *Definition of Productivity.*—The definition of productivity in Section V (*a*) (i) can also be applied to productivity in estuarine bottom deposits. However, as the spatial and vertical variation in productivity of a unit volume of estuarine mud varies enormously (ZoBell 1946) the practical difficulties in direct estimations of protoplasmic content are such as to render this approach impossible.

In the study of the bottom deposits of Australian estuarine systems, an effort has been made to establish relationship between the concentrations of certain forms of phosphates, and in particular the adsorbed phosphates, and the carbon and nitrogen contents. These latter properties have been assumed to be proportional to the protoplasmic content of the mud. The turnover in the phosphatic content would then provide an indication of protoplasmic turnover and hence of productivity. However, the method can only be an approximation for a number of reasons:

(1) The exchange of phosphatic and protoplasmic constituents between the mud and the overlying waters can be quite considerable (Section VI (*b*) (iii)).

(2) The exact role played by the various forms of phosphate present in the mud protoplasmic production is not known.

(3) There cannot be disregarded the possibility that only a small portion of the carbon-nitrogen content is in the form of protoplasm, the remainder occurring as soil humates or their marine equivalent (Waksmann 1933), which do not play a part in the carbon metabolism of the mud.

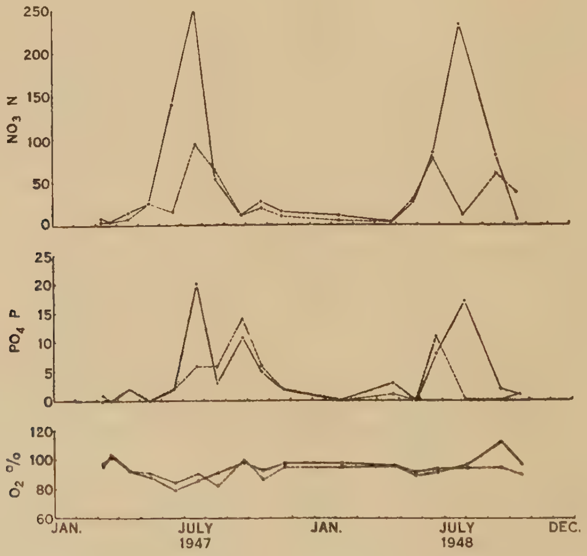

Fig. 55.—Seasonal cycle of nitrate N, phosphate P, and O_2 percentage saturation at Station 3, Swan River, 1947-48.

●—● Surface data. ●- -● Bottom data.

(ii) *Interrelationships of Constituents in Estuarine Bottom Deposits.*—In Table 11 are given the ratios between certain constituents of estuarine bottom deposits. These ratios are grand means of all the data available for the particular hydrological zone of the system. The zonal variation in the C/N ratio has been discussed in Section III (*b*) (iii) (6).

The organic carbon to total ferric iron ratio is generally higher towards the marine end of the system. The greater organic carbon accessions to the bottom deposits from the waters of the marine zone, in combination with the low ferric iron values encountered in the same zone, are probably responsible for the zonal variation in this ratio.

The general organic carbon to adsorbed phosphate ratio varies in a somewhat regular fashion from freshwater to marine zones. The maximum value is always found within the marine or tidal zone, and often considerable interzonal variation is encountered. The numerical value of this ratio is to be compared with that in the open sea.

TABLE 11

INTERRELATIONSHIPS OF CHEMICAL CONSTITUENTS IN AUSTRALIAN ESTUARINE MUDS

System	Zone	No. Obs.	C/N	C/Fe	C/Adsorbed P	Fe/Total P
George's R. and Botany Bay	Freshwater	(4)	17.6	0.8	600	80
	Gradient	(9)	10.7	1.0	400	60
	Marine	(9)	12.6	4.1	500	50
Port Hacking	Gradient	(15)	22.0	3.1	1700	40
	Marine	(16)	14.3	2.8	2400	30
Hawkesbury R.	Freshwater	(18)	16.5	1.7	600	130
	Gradient	(31)	17.6	2.0	600	120
	Tidal	(7)	13.58	1.3	1400	40
Manning R.	Freshwater	(8)	11.6	0.9	400	70
	Gradient	(10)	10.9	0.5	270	80
	Tidal	(12)	10.7	1.5	1200	50
Macleay R.	Freshwater	(10)	10.8	0.4	210	70
	Tidal	(21)	11.2	0.8	300	120

According to the data given by Sverdrup, Johnson, and Fleming (1942), the organic carbon to inorganic phosphate ratio varies for oceanic waters between extreme values of 280 and 28,000, with an average of 2,800. Assuming that the adsorbed phosphate in the mud is the productivity equivalent of the inorganic phosphate content of the seawater, the value of 2,400 for the muds of the Port Hacking marine zone is of a comparable order. This agreement does infer that the assumption made in Section VI (*b*) (i) (regarding the role of adsorbed phosphates in mud metabolism) is not without justification.

The variation in the ferric iron to total phosphate ratio is probably due more to zonal variation in the ferric iron content, rather than to variation in the total phosphate content. These ratios, in spite of the lack of available data and their rather narrow geographical distribution, do show a fairly consistent interzonal trend, and suggest that the properties of the bottom deposits are influenced by the zonal hydrological properties of the overlying water, in spite of large geographical variations in the compositions of the edaphic silt that forms their basic structure.

(iii) *Exchange of Nutrients between Muds and Water of Estuarine Systems.*—Mortimer (1941, 1942), in an extensive investigation of the factors governing exchange of nutrients across the mud-water boundary in freshwater lakes, has shown the important role played by redox potential levels in desorption-adsorption phenomena. The redox potential, by changing the relative proportions of ferrous and ferric forms of iron, is able to control the retention of nutrients, and in particular, phosphates, within the mud or water phase of the cycle. The development of reducing conditions in the mud, below a redox potential of $E = -0.20$ mv., is largely a function of the oxygen content of the water and of the mud porosity.

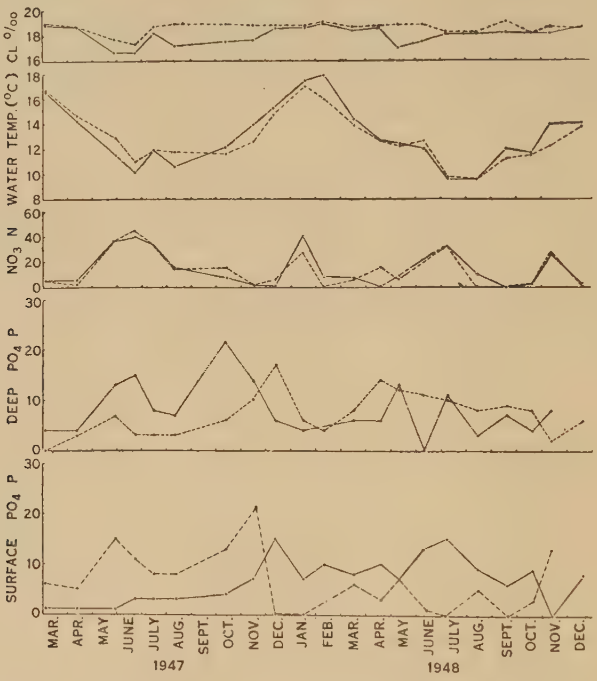

Fig. 56.—Seasonal cycles of hydrological properties at Gordon, D'Entrecasteaux Channel, Tasmania, 1947-48.

Chlorinity, temperature, nitrate N.

●—● Surface data. ●- -● Bottom data.

Phosphate P

●—● Surface inorganic P. ●- -● Bottom inorganic P.

●- · -● Surface organic P. ●. .● Bottom organic P.

In Australian estuarine systems, similar exchanges could conceivably occur in the deeper basins of the marine zone, in which a persistent summer turnover of nutrients, and especially phosphates (Section VI (*a*) (iv)), occurs in the bottom waters. However, water movement and mixing exchanges rarely permit deoxygenation of these waters to develop to a sufficient degree, and for a sufficient period of time, for reducing conditions to become established. It is considered that if desorption of nutrients adsorbed on bottom mud particles does occur in Australian estuarine systems, biological control of redox potential, such as has been found by ZoBell (1946) with bacteria, is the more likely regulating mechanism.

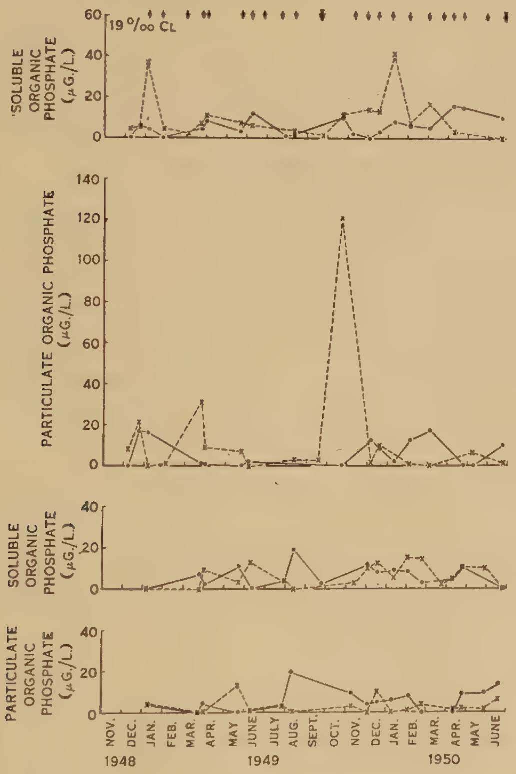

Fig. 57.—Seasonal variation in soluble and particulate organic phosphates in the waters at Station 4 (upper half) and at Station 1 (lower half) of the Port Hacking system. In all cases the dashed line represents bottom and the full line surface values. The arrows at the top of the figures denote departures from a Cl°/oo figure of 19°/oo. Arrows pointing downwards indicate a lowering and upwards an increase of this figure.

At the present stage of these estuarine studies, the material available for an examination of such exchange relationships is limited in quantity. However, it is possible to arrive at certain general conclusions. In the deep basin of the Port Hacking system, the cycles of mud conditions

(Fig. 62) and of water nutrients (Fig. 46) possess certain similarities. Comparing the 1949 cycle of deep inorganic phosphates in the water and the adsorbed content of the surface mud, it can be seen that the occurrence of peaks and minima approximately coincide. A scatter diagram (Fig. 64) demonstrates this relationship more clearly. Although the number of observations is insufficient to permit of accurate diagnosis of the cycle of interaction, the following hypothesis is advanced and will be subjected to critical appraisal as the data are accumulated.

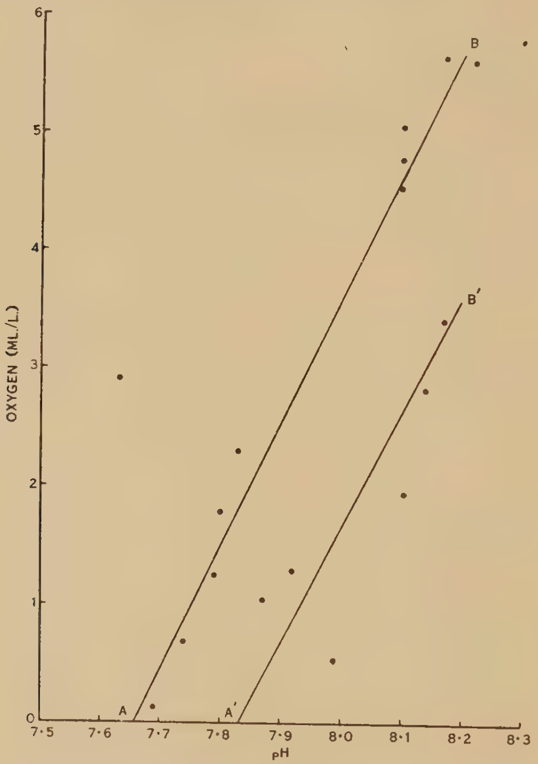

Fig. 58.—Relationship between the pH and the dissolved oxygen content of the bottom waters at Station 4, Port Hacking.

As the content of inorganic phosphates in the water increases to level *B*, the phosphate uptake by the mud and retention as adsorbed phosphate, represented by line *AB*, are slow. Above the critical level *B*, however, phosphate uptake by the mud is very rapid and is represented by line *BC*. as the inorganic phosphate level in the water decreases, retention by the mud of adsorbed phosphates is effective until the critical level *D* is reached. Then desorption of phosphates is rapid until the initial conditions at *A* are again established. It is evident, however, that much more detailed and intensive sampling in the deep basin of the Port Hacking system will be required to establish the validity or mechanism of this interaction cycle.

Although subject to rather irregular monthly variations, the annual trends for organic carbon and total ferric iron at this station are similar, and exhibit minimum values in January and maximum values in the intermediate period. This is the inverse of the adsorbed phosphate cycle and seems to indicate that the organic and iron content of these muds does not play a major role in any phosphate adsorption-desorption cycle.

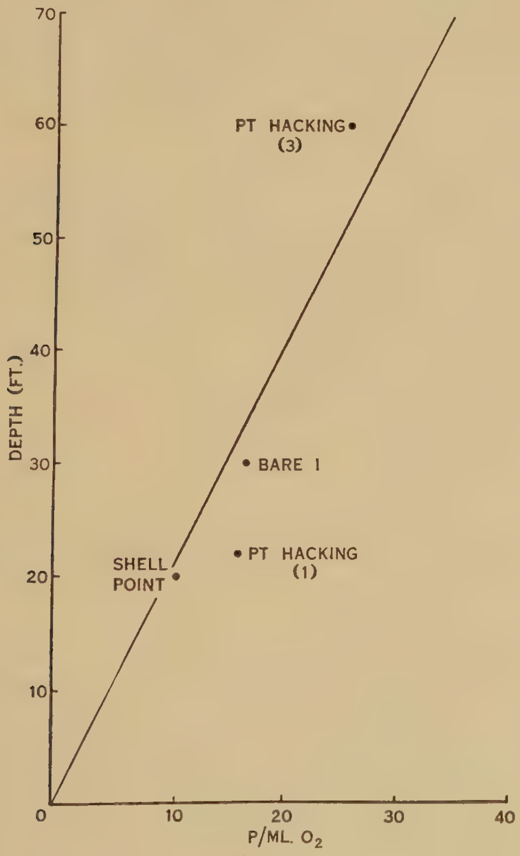

Fig. 59.—Relationship between the water depth and the phosphate liberated per ml. of dissolved oxygen in the bottom waters of some estuarine systems.

In the Macleay River system a relationship is evident between changes in the phosphate content of the water and in the adsorbed phosphates in the mud (Figs. 53 and 65). It is apparent that the flood scouring and silt deposition that occurred in March, July, and November in this system has had some effect on the phosphate content of the mud, and the total phosphate content is a reflection of this (Fig. 65).

The annual cycle for total iron in these muds is in agreement with the adsorbed phosphate cycle, but in the absence of a corresponding annual cycle in organic carbon, any hypothesis concerning the role of such compounds in the adsorption-desorption cycle must await further observations.

It is interesting to note, however, that the average annual content of adsorbed phosphates in these muds is much higher than in the Port Hacking basin, and this is probably attributable to the persistence of phosphates in the waters of the Macleay River system.

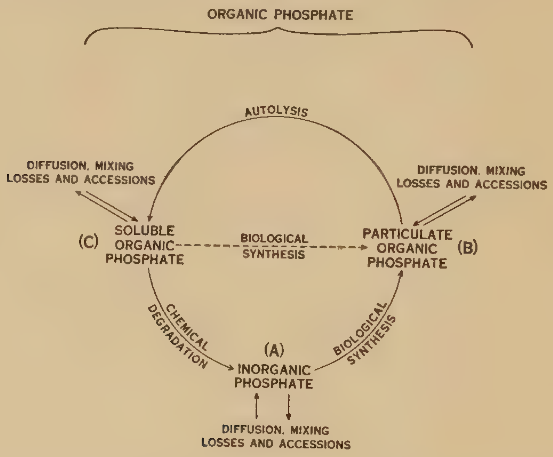
ORGANIC PHOSPHATE
AUTOLYSIS
DIFFUSION, MIXING LOSSES AND ACCESSIONS
DIFFUSION, MIXING LOSSES AND ACCESSIONS
(C)
SOLUBLE ORGANIC PHOSPHATE
BIOLOGICAL SYNTHESIS
PARTICULATE ORGANIC PHOSPHATE
(B)
CHEMICAL DEGRADATION
BIOLOGICAL SYNTHESIS
(A)
INORGANIC PHOSPHATE
DIFFUSION, MIXING LOSSES AND ACCESSIONS

Fig. 60.—A simplified cycle of phosphorus transformations within a relatively isolated water mass, and the respective role of biological synthesis and chemical degradation in such a cycle.

(iv) *Soil Carbon and Nitrogen in Relation to the Carbon and Nitrogen Content of Estuarine Muds.*—Although the role of soil edaphic factors in the development of carbon and nitrogen levels in the bottom deposits of Australian estuarine systems is not exactly known, it is conceivable that the content of these constituents in the drainage soils of an estuarine system will determine their basic level in the system. Subsequently these levels, as demonstrated in Section III (*b*) (iii) (3), are modified by the varying degree of planktonic activity in the overlying water. Rawson (1941) has shown the importance of such edaphic factors in biological productivity level of Canadian lakes. Pearsall and Pennington (1947), in discussing the origin of the organic matter in the bottom deposits of Lake Windermere, were able to show the importance of changing agricultural practices in the development of organic horizons in the bottom profiles. They stressed, however, that in the final phase the composition of such organic matter, as expressed by the C/N ratio, is largely a function of local climatic factors and the trophic level of the lake concerned.

There is a paucity of carbon and nitrogen analyses of soils from the drainage areas of New South Wales estuarine systems, and the data in Figure 66 have been compiled from available sources (Parbery 1936, 1939). In pedology it is accepted that there is a crude inverse relationship between the absolute nitrogen content and the C/N ratio (McLean 1930).

From Figure 66 it can be seen that the New South Wales coastal soil data in the main conform to this relationship (trend line AB). On the same scatter diagram, the mean C/N ratios and absolute nitrogen levels of muds from the marine zone of New South Wales estuarine systems (Table 12) are plotted. It is apparent from this diagram that some muds are identical in this property with New South Wales coastal soil whenever their C/N ratios lies above a base level of 12.

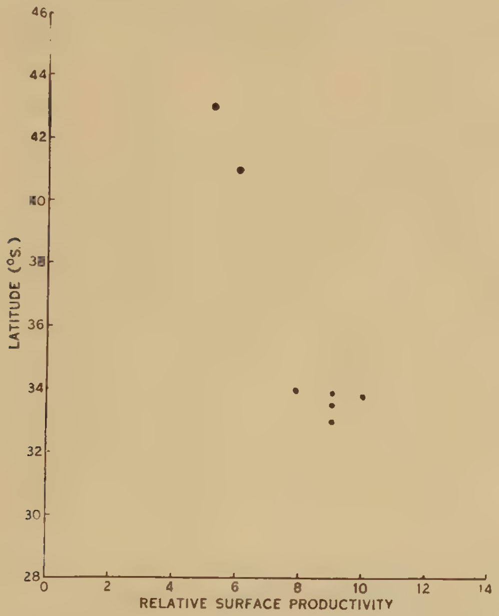

Fig. 61.—Relationship between the relative surface productivity of estuarine water masses and their latitude.

Below a C/N ratio of 12, no regular variation in this ratio with absolute nitrogen levels can be ascertained. It seems probable, therefore, that the soil edaphic factors do play a part in determining the basic C/N ratio of estuarine bottom deposits of the marine zone, but these basic ratios, as will be discussed in the following section, are greatly modified by the trophic levels of the associated water masses.

(v) *Relative Productivities of Estuarine Muds.*—Table 12 gives the mean values of all data so far available on the chemical composition of Australian estuarine (marine zone) bottom muds. The Shell Point data from the tidal zone are given for comparison. A plot of the relationships of adsorbed phosphate to total nitrogen and to organic carbon (Fig. 67) demonstrates quite clearly, in spite of the limited number of observations available, that the adsorbed phosphate and carbon contents of these muds are fairly closely related.

If it were possible to assign a productivity significance to absolute levels of organic carbon, then the demonstration of the control of relative productivities of bottom muds by adsorbed phosphate would be a reasonable possibility. However, some bottom muds of the marine zone have carbon and nitrogen levels and relationships suggestive of direct soil origin, and the influence of local *in situ* biological activity is difficult to determine.

TABLE 12

MEAN CHEMICAL COMPOSITION OF BOTTOM MUDS AT SELECTED STATIONS WITHIN THE MARINE ZONE OF EASTERN AUSTRALIAN ESTUARINE SYSTEMS

System	Station	No. of Obs.	Int. P	Adsorbed P	Total P	Total Ferric Iron	Organic C	Total N	C/N	Silt (%)
Richmond R.	3	1	5	5	461	105.0	16.2	1.12	14.5	14
Macleay R.	1	1	2	62	560	32.0	24.0	1.56	15.4	18
Pt. Stephens	Nelson's Bay	1	1	23	437	22.3	25.0	2.7	9.3	8
Hawkesbury R.	3	5	8	96	700	26.9	68.6	3.46	19.5	34
Botany Bay	1	7	1	66	689	8.8	26.66	2.34	11.4	7
Shell Point	10	19	4	60	504	40.7	48.5	3.68	13.2	23
Pt. Hacking	3	11	3	45	734	21.8	57.25	4.24	13.5	11
Tamar R.	1	1	3	3	192	12.0	6.0	1.6	3.8	9
Derwent R.	1	1	2	15	252	11.7	21.0	3.6	5.9	1.5

In pedology, the carbon to nitrogen ratio is considered an index of the efficiency of carbon fixation relative to absolute nitrogen levels, and within limits the higher the ratio the more productive is the soil. If we examine the relationship between the adsorbed phosphate content and the C/N ratio of these marine zone muds (Fig. 68) an almost linear relationship, except for the Richmond River values, is apparent.

On the data so far available, therefore, it seems probable that the adsorbed phosphates can be considered as important limiting factors in controlling the absolute levels of carbon and of nitrogen in marine zone muds. It is impossible at this stage of the investigation, however, to assign productivity significance to the adsorbed phosphate content, although the stimulation in metabolic activity and growth rate of oysters, as the result of phosphate enrichment of such muds (Section VIII) is reasonably conclusive regarding their importance.

In Figure 69, the relationship between the C/N ratio of bottom muds and the relative productivity level (Section VI (*a*) (v)) of the associated water masses has been plotted. There is some suggestion of a direct relationship between these two productivity indices such that high water productivity is associated with a high C/N ratio. This is further evidence in support of a continuous exchange of trophic elements between the mud and water in an estuarine system, the principle of which has been examined in Section VI (*b*) (iii).

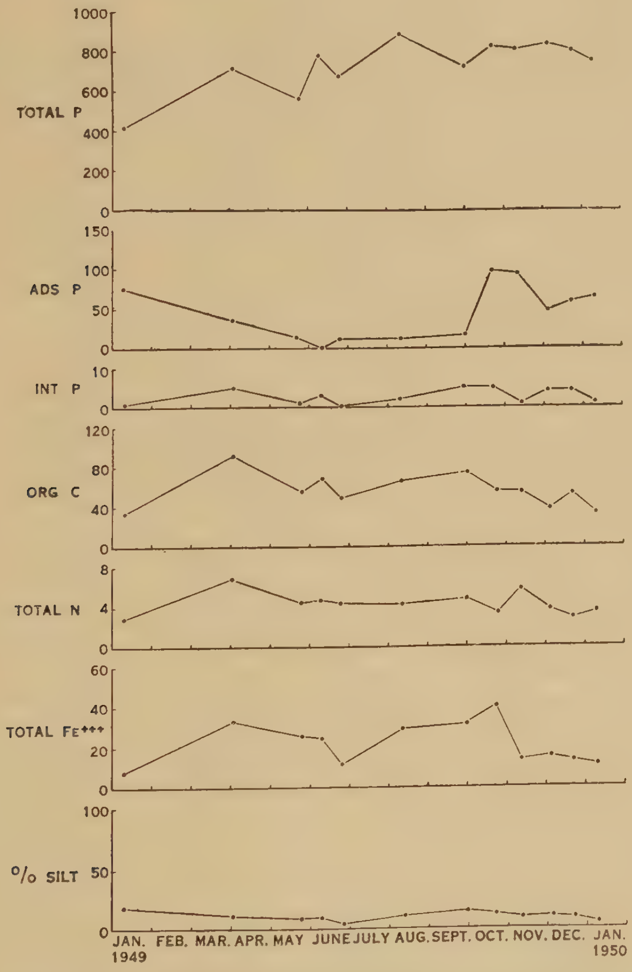

Fig. 62.—Seasonal cycle of bottom properties at Station 4, Port Hacking, 1949.

Table 13 shows a calculation of the amounts of adsorbed phosphates in the bottom muds of the marine zone, relative to the mean inorganic phosphate content of the associated water masses.

Assuming that the adsorbed phosphate in these muds does determine to some extent its basic productivity level, it is clear, in spite of our lack of knowledge of relative rates of turnover of phosphates in the mud and water, that immeasurably greater quantities of phosphates are capable of entering into this cycle in the former medium.

It is clear, however, that a good deal of basic information on phosphate and other metabolic cycles in estuarine muds must be obtained before a full examination of the relative productivities of estuarine muds and water can be attempted.

TABLE 13

MEAN INORGANIC AND ORGANIC PHOSPHATES IN THE WATERS, AND ADSORBED PHOSPHATES IN THE MUDS, OF CERTAIN CENTRAL NEW SOUTH WALES ESTUARINE SYSTEMS

System	Port Hacking	Botany Bay	Hawkesbury R.	Pt. Stephens
Mean annual inorganic phosphate P	6 mg./c. metre	5 mg./c. metre	14 mg./c. metre	6 mg./c. metre
Approx. volume of marine zone	63 x 10^6 c. metres	37 x 10^6 c. metres	97 x 10^6 c. metres	312 x 10^6 c.metres
Total mean annual quantity inorganic phosphate P in marine zone	378 g.	185 g.	1358 g.	1872 g.
Mean annual organic P	8 mg./c. metre	9 mg./c. metre	9 mg./c. metre	9 mg./c. metre
Total mean annual quantity organic P in marine zone	504 g.	333 g.	873 g.	2808 g.
Mean adsorbed P in bottom mud (mg./100 g. mud)	0.5 mg.	0.5 mg.	3.3 mg.	0.2 mg.
Weight mud to equal total P in water	75.6 x 10^6 g.	37 x 10^6 g.	41.2 x 10^6 g.	935 x 10^6 g.
Surface of mud with depth of 10 cm. to contain above wt. of mud (S.G. mud = 1.5)	59 x 10^5 sq. cm.	25 x 10^5 sq. cm.	27.4 x 10^5 sq. cm.	62.3 x 10^5 sq. cm.
Total mud surface in marine zone	6.6 x 10^6 sq. yd.	24 x 10^6 sq. yd.	25.6 x 10^6 sq. yd.	52 x 10^6 sq. yd.
Ratio adsorbed P in upper 10 cm. mud to inorganic P in water of marine zone	7,800	26,000	55,000	2,400

VII. Applications of Estuarine Hydrology to Oyster Cultivation

Although some sections of the waters of the marine zone of estuarine systems possess environmental stability, and hence productivity characteristics similar to those of the adjacent neritic waters, the bottom deposits of the tidal zone of estuarine systems appear to be a more stable milieu for persistent organic productivity than are the waters of that zone. The work of Reid (1929) has shown the resistance of beach sands to variation in the chlorinity of their interstitial fluids, despite big changes in the chlorinities of their associated water masses. Although similar investigations on the sandy bottom deposits of Australian estuarine systems have not been made, it is reasonable to assume that they will exhibit similar stability of the chlorinity environment.

The compactness of the flocculent muds of the tidal and gradient zones renders it likely that, beyond the upper several inches, changes in the composition of the interstitial fluid in response to changes in the properties of the overlying waters would be damped out and practically insignificant. In the upper tidal and gradient zones, where the water

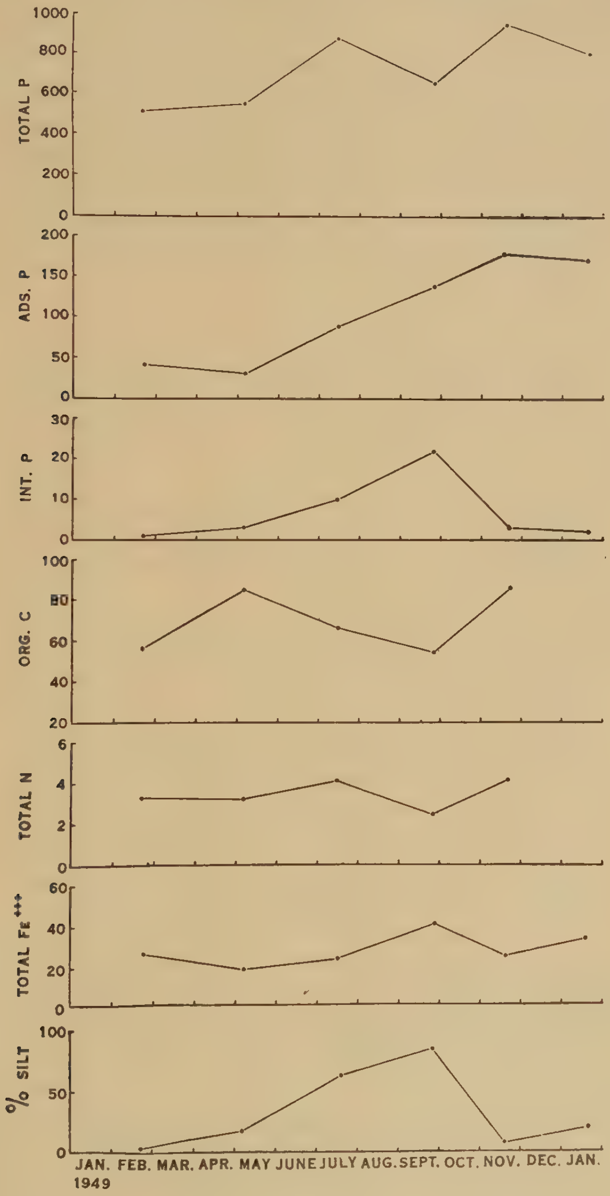

Fig. 63.—Seasonal cycle of bottom properties at Station 3, Hawkesbury River, 1949.

environment is particularly unstable, a mud biota could become established and develop in a comparatively stable milieu at some distance below the mud surface.

In the tidal zone of most estuarine systems, productivity seems to be largely governed by the metabolic activity of the mud biota. It is considered likely that such metabolic activities are governed by availability of trace elements, and in particular of phosphates. Successful oyster fattening is carried out on trays laid out over these flocculent mud flats of the tidal zone. It seemed likely, therefore, that persistent microbiological turnover on these mud flats could provide a considerable proportion of the food substances necessary for such oyster fattening.

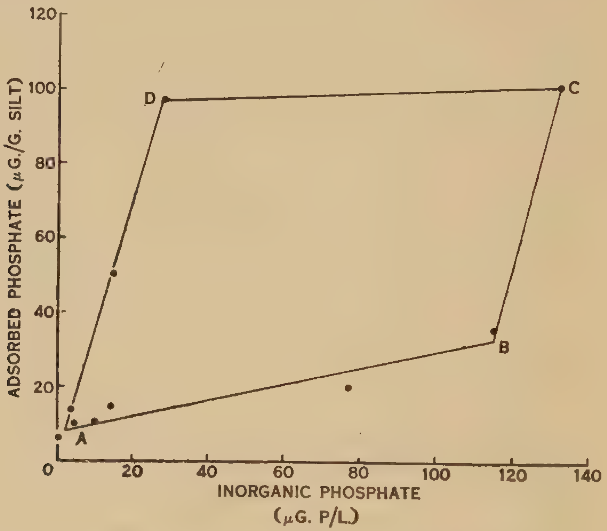

Fig. 64.—Relationship between the adsorbed phosphate of the mud and the inorganic phosphate content of the overlying water mass, in the bottom regions of Station 4, Port Hacking.

In an endeavour to stimulate the growth rate of oysters, the enrichment of the intertidal zone of such flats by a phosphatic proteinaceous fertilizer was carried out at Shell Point, George's River, in late 1947.

At low tide the enrichment mixture, consisting of equal parts of superphosphate and linseed oil meal, was broadcast over the flats and raked into the surface layers of a small plot at the rate of 10 lb. mixed fertilizer per 100 sq. yd. Although undoubtedly some of this enrichment mixture was lost by leaching in the succeeding tidal movement of water over the flat, subsequent analyses showed that a large percentage of the added phosphates was adsorbed on the mud particles. From the results of the carbon analyses, however, it was apparent that a good deal of the linseed oil meal sank to deeper levels in the mud and was unaffected by leaching. The broadcast technique has recently been abandoned in favour of fertilizer placement in small plots enclosed by wooden sides. By this means the enrichment mixture can be placed at the right depths below the surface to suffer almost negligible loss by leaching, while still remaining within the mud trophic level. From such plots, provided they are placed in correct relationship to water movement, it is assumed that food substances will be carried to the oysters.

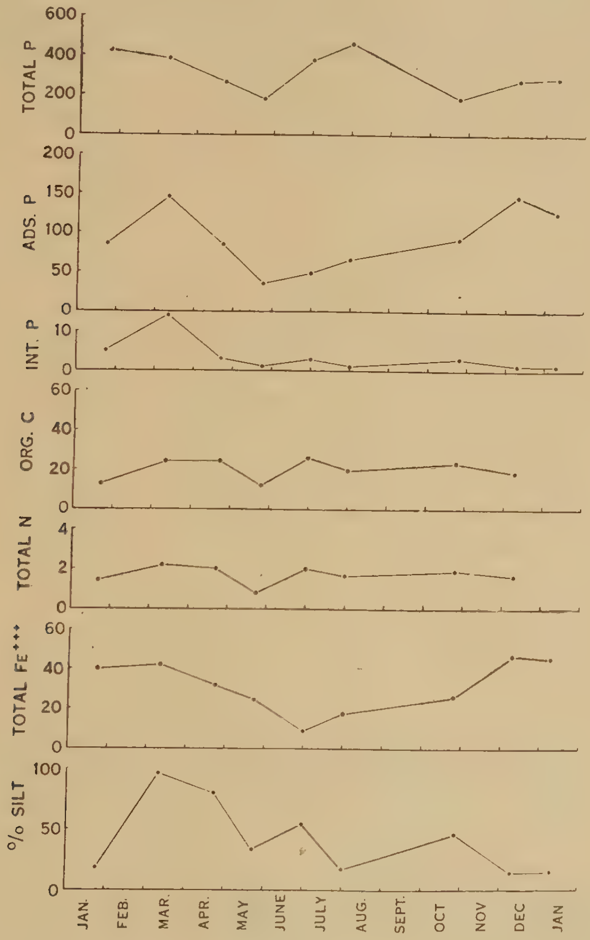

Fig. 65.—Seasonal cycle of bottom properties at Station 2, Macleay River, 1949.

Although a good deal of commercial evidence has been accumulated in favour of this enrichment treatment of mud flats, a final decision based upon the long-term measurements of the comparative growth of selected oyster stocks in enriched coastal areas is not yet possible. In Figure 70 the whole weight and specific gravity determined as the quotient of whole weight to displacement volume have been plotted of oysters grown over the enriched and control plots at Shell Point.

Station 1 was situated at the optimum growing region near the low water ordinary spring tides, and was fertilized. Station 2 was situated at a mid-water and less suitable growing region, and was also fertilized. Station 11 was situated in the same growing region as Station 1, and not being fertilized, was considered as a control on Station 1. Station 12 lay at the same growing region as Station 2, but was unfertilized and hence presumably could provide a control on results from this station. It was clear, however, from the chemical analyses of the mud flat, that some interchange of enriched silt, or more probably a dispersal of the organic end products of fertilizer placement, was occurring between Stations 1 and 2 and their controls. Moreover, the difficulty experienced by Humphrey (1941) in reducing the sampling error involved in the proximate analyses of oyster meats, the unreliability of whole oyster weight as a measure of meat content, and the effect of persistent handling on growth, impose further limitations on the interpretation of the data presented in Figure 70. Nevertheless, the growth curves exhibit certain significant features. At all times the mean whole weight of the oysters at Station 1 was considerably higher than that for the control Station 11. This is particularly marked in the 1949 growth curves. Secondly, it is of interest to note that, although the mean growth rate of oysters at Station 2 in 1947-48 was not persistently higher than that at control Station 12 during 1949, a rise

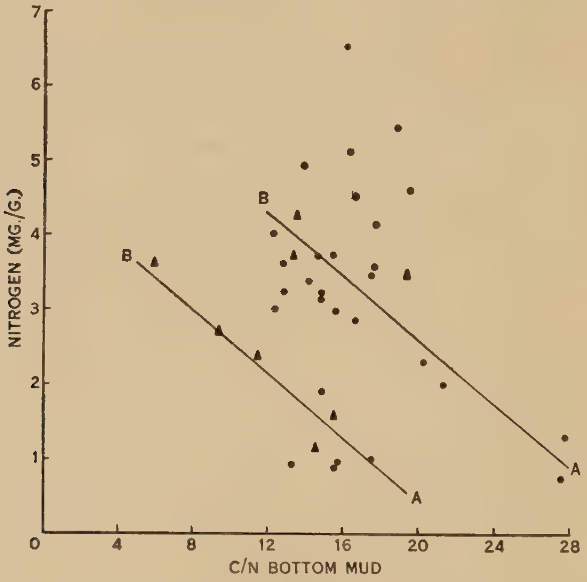

Fig. 66.—Relationship between the nitrogen level and the C/N ratio of New South Wales coastal soils (plotted as dots) and between the nitrogen level and the C/N ratio of New South Wales estuarine muds (plotted as triangles).

in mean growth rate to a level comparable to that at Station 1, and much superior to the control station growth, was in evidence.

According to the specific gravity curves, the difference in growth rates between Stations 1 and 2 and their controls in 1949 has been accompanied by a persistent decline in this property at the former station. This is assumed to mean a greater development of the lighter meat compared with the heavier shell content of the oysters at Stations 1 and 2 during the same period. Some further evidence on internal weighing and examination for meat condition during the same period will shortly be available, and will be published in a forthcoming paper on enrichment studies. It is evident, however, that a comprehensive normal oyster growth rate level must be established for a particular region, and that the effect of enrichment on subsequent growth rates must be compared with such a level to obtain a clear-cut demonstration of the commercial possibilities of such treatment. Such a method is now being followed within selected New South Wales estuaries.

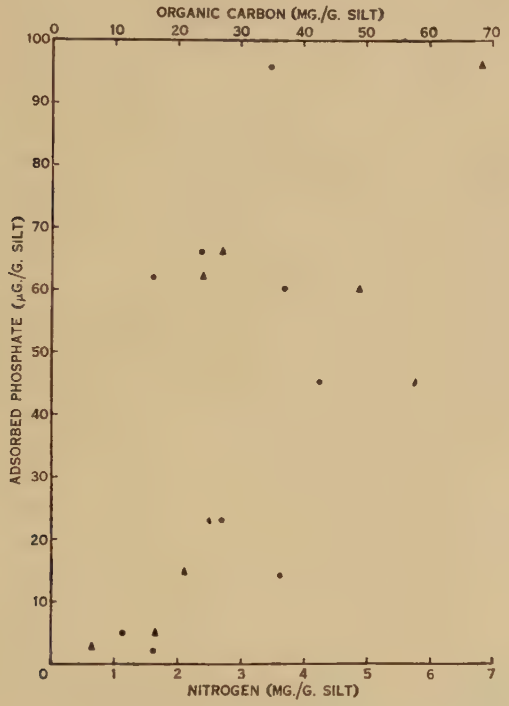

Fig. 67.—Relationship between the mean adsorbed phosphate and nitrogen content (plotted as dots) and between the mean adsorbed phosphate and carbon content (plotted as triangles) of estuarine bottom muds. The data are taken from Table 12.

The stimulation of oyster growth by the chemical enrichment of its substrate would provide a convenient commercial method of increasing meat yield, and enable the oyster farmer to exercise control over this important phase of his activities.

The role of plankton organisms in the food supply of lamellibranchs and oysters has been recently discussed by Korringa (1949). It is quite conceivable that the principal effect of chemical enrichment of the bottom mud substrate is the stimulation of microbenthic turnover and an increase in the amount of detrital organic matter circulating in the overlying waters. In estuaries, such a method of stimulation is considered more economically feasible than the method of direct fertilizing of the water used by Gross *et al.* (1944) in the Loch Craighlin experiments. The spreading and mixing of any chemical fertilizers added to the water in any particular locality of an Australian estuarine system would be of such a magnitude as to render negligible any local effect on productivity. On the other hand, the chemical retention of the bulk of such fertilizers by the mud, as demonstrated by Breest (1921) in pond studies, and their persistent long-term effect on local productivity, makes mud enrichment more economically justifiable.

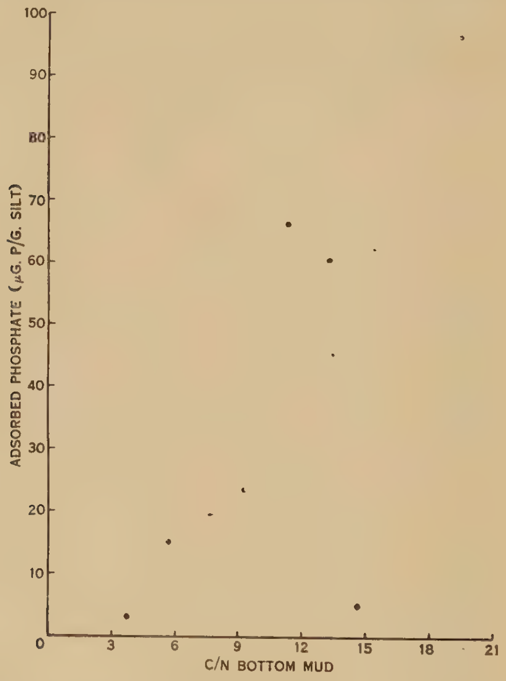

Fig. 68.—Relationship between the adsorbed phosphate content and the C/N ratio of estuarine bottom muds.

A more profitable approach to the problem of increased oyster growth rates would seem to lie in the use of enclosed bodies of estuarine waters capable of bottom enrichment at periodic intervals. This method would be an adaptation of the tanbak cultivation of Indonesia (Schuster 1949) and, provided some degree of control were exercised over the physical and chemical properties of the hydro-environment, should result in greatly increased growth rates of oysters cultivated in such a situation. The practical aspects of such a technique are now being investigated on a semi-commercial scale.

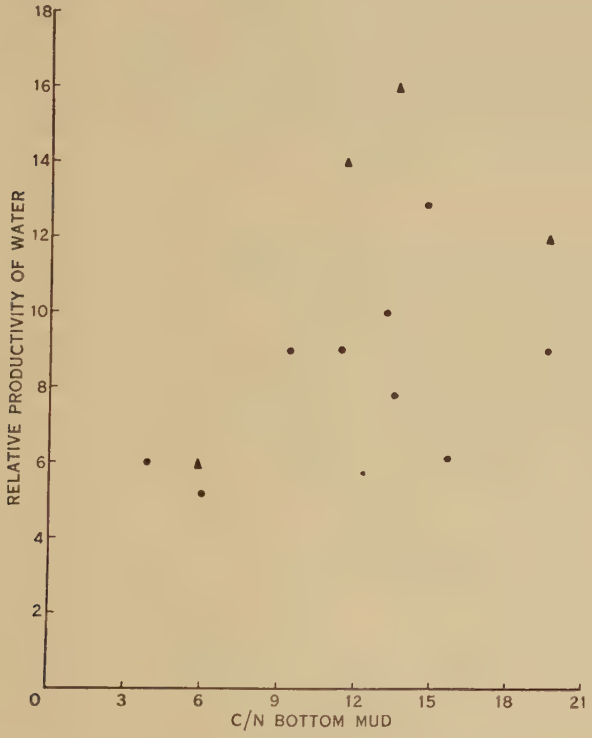

Fig. 69.—Relationship between the relative productivity of an estuarine water mass and the C/N ratio of its bottom mud. ● Surface productivity. ▲ Bottom productivity.

On the basis of zonal dominance it is possible to differentiate between estuarine systems, e.g., Port Hacking, in which only the spatting phase of oyster cultivation is successful, and others, e.g., George's River, in which only the growing phase of such cultivation can be undertaken.

The former system is marine-dominated, and it has been found in all systems investigated that only within the marine zone can a commercially useful spat fall be expected. It is considered likely that the food requirements of the oyster larva can only be met by a readily available supply of small, naked flagellates, whose existence in relatively enormous quantities has been recently demonstrated in the open sea (Atkins 1945). The almost neritic characteristics of the marine estuarine zone favour the development of such organisms, and the voracious oyster larvae living in such a water mass are able to obtain sufficient food to grow to maturation and settle as spat. In the tidal zone, the extensive tidal mud flats, on which oyster fattening is carried out, do not provide a suitable environment for the persistent turnover of these naked μ flagellates in the water mass, and the oyster larvae die of starvation before reaching maturation. On the other hand, as discussed earlier in this section, the nutrient richness of these mud flats is capable of sustaining a persistently high crop of microbiota in the mud surface. These microbiota form the initial section of a food chain for the growing oysters. The demonstration of a recurrent population of tintinnids over the mud flats of the tidal zone in the George's River (Appendix IX) is highly suggestive in this regard.

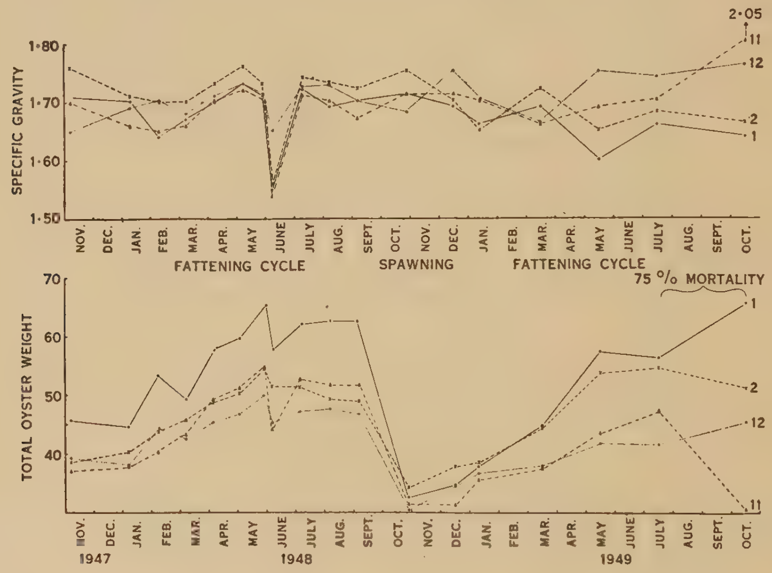

Fig. 70.—Seasonal variation in total weight and specific gravity of groups of 36 oysters grown over enriched and control plots at Shell Point, George's River.

The variation in the geographical location of the chlorinity conflict, and the relation of the latter to the gradient estuarine zone, could be very important in the estuarine penetration of sessile marine invertebrates, e.g., molluscs, annelids, polychaetes. With the Sydney rock oyster, *Ostrea commercialis,* living specimens have been found at low chlorinity levels within the gradient zone of some of the central New South Wales systems. These specimens were generally in poor condition, with thickened and distorted shell growth. While this lack of growth is probably due in part to absolute chlorinity levels, the diurnal cycle in this property is considered equally as important. Thus in the George's River system, with a well-developed Cl°/oo conflict in the gradient zone, natural oyster growth ceases above Station 10 (Fig. 18) situated 11·6 miles from the mouth.

In the Hawkesbury River, on the other hand, with a less pronounced Cl°/oo conflict in the gradient zone, natural oyster growth can be detected to about Station 10 (Fig. 23) with a lower chlorinity and at a distance of 17.5 miles from the mouth.

While the gradient zone of the latter system possesses a greater degree of annual Cl°/oo stability (Section V (*c*) (v)), it is considered more likely that, in the George's River system, natural oyster growth would develop at the same low Cl°/oo value if the diurnal Cl°/oo conflict were less. The varying effect of the absolute and rapid diurnal changes in Cl°/oo on estuarine faunal and floral distribution provides a field for experimentation by the comparative physiologist.

VIII. Discussion and Conclusions

In this paper an attempt has been made to introduce a new concept of estuarine hydrology, that of a hydro-biological system which, by reason of varying isostatic and tidal pressure from its fluviatile and neritic sources, develops certain hydrological zones, the volumes of which in the main determine its environmental and productivity characteristics. Moreover, in this concept, the influence of bottom characteristics on the productivity of estuarine water masses is considered highly important, and much more so than in shallow neritic or lacustrine waters.

The rather peculiar cellular circulation developed in most eastern Australian systems (Section IV (*c*)) is responsible for the rapid interchange of nutrients and elements of the mud microbenthos between the mud and the overlying water mass.

The cycle of phosphates in the water mass at Station 3, Port Hacking (Section VI (*a*) (iv)), and its relationship to corresponding cycles in the mud (Section VI (*b*) (iii)) is considered typical of that occurring in any semi-isolated waters of the marine or lower tidal estuarine zones.

The *modus operandi* of this exchange cycle between the mud and water cannot as yet be demonstrated, although it is clear that the development of bottom reducing conditions such as Mortimer (1941, 1942) found in his lacustrine studies, could not be as effective (Section VI (*b*) (iii)).

The probability is that the metabolic activity of the local microbenthos determines the redox potential of the bottom mud (ZoBell 1946) The metabolism of the microbenthos is governed *inter alia* by the supply of phosphatic nutrients, so that an interrelated local cycle of phosphatic exchange of the type demonstrated in Section VI (*b*) (iii) could be developed in this fashion. The threshold values at *B*, *C*, and *D* in Figure 64 could then be related to biologically determined adsorption-desorption conditions in the mud.

The positioning of the hydrological zones according to the identifying properties of Section V (*c*) (i) enables a satisfactory hydrological classification to be adopted for Australian estuarine systems in terms of their relative zonal composition (Section V (*d*) (iii)). The relation of these hydrological zones to oyster spatting and fattening has been discussed in Section VII, but the general ecological applications of such a method of estuarine classification have not been investigated.

The zooplankton of the Hawkesbury River (Appendix VIII) appears to be associated with the hydrological zones of this system. It is quite probable from such field observations as have been made that the distribution of *Zostera, Gracilaria,* and mangroves is determined by the zonal composition of a system. For example, it is considered likely that *Gracilaria* is limited in its estuarine penetration by the marine-tidal zone boundary. *Zostera,* on the other hand, is confined to the tidal zone. Mangroves appear to be distributed in the lower end of the gradient zone with the extent of penetration towards the freshwater zone quite variable. It is suggested that the characteristics of the bottom substrate are more important in the development of this distribution pattern than those of the water.

In the marine zone, a continual supply of interstitial phosphates is available in the upper portion of the sandy muds of this region and could provide a phosphate supply for the shallow-bedded and almost rootless *Gracilaria.* In the tidal zone the lesser quantities of such interstitial phosphates, and the more densely compacted muds, could enable the more deeply rooted *Zostera* to flourish. The mangroves, on the other hand, are considered to be associated with the phosphate-rich muds of the upper gradient zone (Section V (*b*) (iv)) and their successful development in this area is a balance between the richness of the phosphate supply and the rigours of the chlorinity environment. It is evident, too, that the composition of the macrobenthos as represented by the polychaetes, the annelids, the molluscs, and the crustacea varies qualitatively from one estuarine zone to the next. In the marine zone a preponderance of the soft-bodied chaetophorous forms is encountered. In the tidal zone molluscs and small soldier crabs appear to be the dominant forms. There is, however, an almost complete absence of any biological data by which a quantitative evaluation of these relationships could be adduced. A profitable field for the comparative ecologist would be in such a study of the zonation of the fauna and flora of estuarine systems.

The suggestion in Section VIII that conflict values in estuarine systems play an important role in the determination of estuarine faunal and floral composition is one that needs attention by the comparative physiologist. The food intake by a fixed, sessile organism such as an oyster must be affected by the intensity and rate of change in hydrological properties of its milieu. It has been clearly shown for American oysters (Hopkins 1936) that adjustment to a normal pumping rate after a lowering of salinity is much slower than after an elevation.

In discussing his results Hopkins (1936, p. 361) states that "The rate at which the gills pump water from which food particles are filtered, depends upon the salinity of the medium or more accurately stated, upon the frequency, amplitude and duration of changes in salinity."

This latter property of the salinity environment is more accurately measured by the Cl°/oo conflict value than by the slow seasonal cycles of chlorinity, for which variations sufficient time is often available for successful adaptation. Moreover, as discussed in Section V (*a*) (iv), restoration of an equilibrium chlorinity value is often quite rapid, so that the oyster can withstand such salinity changes by closure of the shell and cessation of feeding.

The estimation of absolute and relative organic productivities in estuarine waters is complicated by a number of factors. There is firstly the suspicion that much of the persistent productivity in estuarine waters is effected by a specialized microbenthos confined to a narrow water-mud stratum; the organisms of this microbenthos are able to withstand the scouring and environmental changes caused by varying freshwater pressure better than are the normal planktoners, such as are responsible for the bulk of organic production in neritic waters. Secondly, there are practical difficulties in the way of sampling this microbenthos, although the pump collections at Shell Point (Appendix IX) provide a partial solution. It is possible that the perfusion method of Lees and Quastel (1946), by which the metabolic activities of soils can be studied, would yield important information on microbiological activity within this estuarine mud substrate.

The method followed in Section VI (*a*) (v), of estimating water productivity by the relative proportion of inorganic to organic phosphate in relation to the inorganic phosphate level, is complicated by the necessity of making several assumptions. Firstly, one must assume that organic phosphates *per se* are not utilized as a phosphate source, as has been found in culture experiments by Chu (1946). Secondly, a considerable degree of seasonal isolation of the water mass must be postulated. This assumption is possible only to a limited extent in certain regions of the marine zone of eastern Australian systems. Absolute levels of inorganic nutrients *per se* have no comparative meaning in estuarine productivity studies.

Turbidity, scouring, and rapid tidal circulation, together with the less stable environment, preclude any direct correlation between inorganic nutrients and plankton production such as has been demonstrated for the George's Bank by Riley (1946).

It is apparent, therefore, that some form of direct chemical assessment should be investigated in estuarine studies. In oceanic waters, Redfield, Smith, and Bostwick (1937) have shown the importance, in productivity estimations, of the absolute levels and rates of turnover of inorganic and of soluble and particulate organic phosphates in the Gulf of Maine waters. It is probable that more concentrated effort on the seasonal distribution of estuarine particulate and soluble organic phosphates, discussed in Section VI (*a*) (iii), will yield similar information on Australian estuarine productivity.

It is apparent from our studies that the assumption of persistent discharge of nutrients by rivers and estuaries into the adjoining neritic waters is not generally true for most of the Australian coastline so far investigated.

Even in the northern New South Wales coastal belt, the flood period is of relatively short duration, and as the bulk of nutrient discharge into the neritic waters occurs during these flood periods, little persistent annual effect can be expected on neritic nutrient levels. The persistent efflux of fluviatile elements into the neritic waters at the mouth of the system such as is common, for example, in Indonesia, India, and in the snow-fed rivers of America, Canada, and northern Europe, is a rare occurrence in Australian coastal waters.

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APPENDIX I

PORT HACKING — STATION LIST

Station Position	Plotting No.	Distance from Mouth (miles)	Station Position	Plotting No.	Distance from Mouth (miles)
Entrance	1	0	Upper South-West Arm	5	4.5
Mouth of Gunnamatta Bay	2	1.5	Mouth of Audley River	6	5.0
Mouth of Burraneer Bay	3	2.5	Mangrove stand	7	6.0
Mouth of South-West Arm	4	3.5	Bend below Audley	8	8.5

APPENDIX II

GEORGE'S RIVER-BOTANY BAY — STATION LIST

Station Position	Plotting No.	Distance from Mouth (miles)	Station Position	Plotting No.	Distance from Mouth (miles)
Off Bare Island	1	0	Picnic Point	12	16.0
Botany Wharf	2	2.0	Upper Woronora River	13	19.0
Mouth of Quibray Bay	3	2.6	Mouth of William's Creek	14	19.5
Quibray Bay	3*a*	3.5	Mouth of Deadman's Creek	15	20.3
Weeny Bay	3*b*	3.8	Millperra	16	21.0
Cook's River mouth	4	4.2	Hollywood	17	23.0
Brighton wharf	5	4.2	Upper William's Creek	18	25.0
Doll's Point	6	4.6	Prospect Creek, Carramar	19	26.0
Shell Point pile	7	5.5	Prospect Creek, Canley Vale	20	27.0
Shell Point	7*a*	5.7	Ingleburn	21	32.0
Gwawley Bay	7*b*	6.0	George's R., King's Fall Bridge	22	52.0
Tom Ugly's Bridge	8	7.0			
Oyster Bay	8*a*	8.5			
Como Bridge	9	9.6			
Lugarno	10	11.6			
Mouth of Salt Pan Creek	11	13.6			

APPENDIX III

HAWKESBURY RIVER — STATION LIST

Station Position	Plotting No.	Distance from Mouth (miles)	Station Position	Plotting No.	Distance from Mouth (miles)
Channel between Hawk Head and Barrenjoey	1	0	Channel at Singleton Mill	13	30.5
Pittwater off Rock Point	2	1.0	Channel at Laughtondale	14	35.0
Bobbin Head, Cowan Creek	3	2.5	Channel at Wiseman's Ferry	15	39.5
Channel between Juno and Challenger Head	4	4.5	Macdonald River	16	45.5
Pittwater off Taylor's Point	4*a*	5.0	Hawesbury River at Portland Ferry	17	51.5
Mullet Creek	5	8.25	Colo River at Upper Colo	18	55.5
Channel under Railway Bridge	6	9.5	Hawesbury R. at Sackville	19	60.5
Mooney Creek	7	11.5	Hawkesbury R. at Clarence Reach	20	69.5
Channel opposite Milson Island	8	13.5	Hawkesbury R. at Windsor	21	78.5
Berowra Creek	9	15.5	Nepean River at East Richmond	22	88.0
Channel off Pumpkin Point	10	17.5	Nepean River at Penrith	23	98.0
Channel off mouth of Mangrove Creek	11	21.5	Nepean River at Camden	24	130.5
Channel Patty's Bight	12	26.0	Cataract River	25	145.5
			Cordeaux River	26	148.0

APPENDIX IV

MACLEAY RIVER — STATION LIST

Station Position	Plotting No.	Distance from Mouth (miles)	Station Position	Plotting No.	Distance from Mouth (miles)
South West Rocks	1	0	Greenhills	6	32.0
Jerseyville	2	5.0	Turner's Flat	6*a*	50.0
Kinchela	3	10.0	Hickey's Creek	7	66.0
Smithtown	4	15.0	Bellbrook	8	82.0
Frederickton	4*a*	21.0	Comara	9	102.0
Kempsey	5	28.0	George's Creek	10	120.0

APPENDIX V

RICHMOND RIVER — STATION LIST

Station Position	Plotting No.	Distance from Mouth (miles)	Station Position	Plotting No.	Distance from Mouth (miles)
East Ballina	1	0	Woodburn	7	28.5
West Ballina	2	2.0	Coraki	8	41.5
Burn's Point	3	5.0	Tathan	9	55.0
Empire Vale	4	8.5	Casino	10	69.0
Wardell	5	12.5	Kyogle	11	90.0
Broadwater	6	17.5	Unungarra	12	114.0

APPENDIX VI

TAMAR RIVER — STATION LIST

Station Position	Plotting No.	Distance from Mouth (miles)	Station Position	Plotting No.	Distance from Mouth (miles)
Low Head	1	0	St. Leonards	7	40.0
Beauty Point	2	5.0	Hadspen	8	42.5
Deviot	3	14.0	Perth	9	56.0
Gravelly Beach	4	18.0	Deloraine	10	69.0
Legana	5	26.0	Epping	11	79.0
Trevallyn	6	33.0			

APPENDIX VII

SWAN RIVER — STATION LIST

Station Position	Plotting No.	Distance from Mouth (miles)	Station Position	Plotting No.	Distance from Mouth (miles)
The Mole	1	0	Narrows	7	12.2
Traffic Bridge, Fremantle	2	2.4	Causeway	8	14.6
			Maylands Jetty	9	17.0
Billy Goat Farm	3	4.4	Smith's Bay	9*a*	19.4
Port Walter	4	6.4	Ascot Bridge	10	21.8
Applecross	5	9.6	McDonald's Dairy	11	23.8
Canning Bridge	5*a*	10.4	Barker's Bridge	12	25.6
Crawley	6	11.0	Upper Swan Bridge	13	30.6

APPENDIX VIII

MACROPLANKTON OF THE HAWKESBURY RIVER SYSTEM

The data in this appendix summarize the results of an investigation of the macroplankton of the Hawkesbury River system, carried out by Miss M. Morris of the Zoology Department, University of Sydney.

The material available for zonal comparison has been blocked out in groups and has been given reference lettering. The chlorinity characteristics of the stations in question can be seen by reference to Figs. 23 and 25. Station 1, at the marine end of the gradient zone, and Station 15, in the gradient end of the freshwater zone, possess maximum environmental stability. Stations 6 and 11 are subject to much greater chlorinity variation.

	Station 1		Station 6		Station 11		Station 15		
	Frequency (%)	Total	Frequency (%)	Total	Frequency (%)	Total	Frequency (%)	Total	
Branchiopoda									
Cladocera									
Penilia	82	404	0	0	0	0	0	0	
Evadne (*a*)	33	412	14	105	0	0	0	0	
Podon	33	8,036	14	130	0	0	0	0	
Daphnia	0	0	0	0	0	0	0	0	
Simocephalis	0	0	0	0	0	0	11	44	
Bosmina	0	0	0	0	20	1,600	33	594	(*b*)
Alona	0	0	0	0	0	0	0	0	
Chydorus	0	0	0	0	0	0	0	0	
Copepoda									
Calanoida									
Nannocalanus	0	0	0	0	0	0	0	0	
Mecynocera	33	120	0	0	0	0	0	0	
Paracalanus	82	9,750	28	809	0	0	0	0	
Acrocalanus (*c*)	16	8,460	0	0	0	0	0	0	
Calocalanus	16	1,386	0	0	0	0	0	0	
Clausocalanus	16	1,166	0	0	0	0	0	0	
Centropages	0	0	0	0	0	0	0	0	
Boeckella	0	0	0	0	0	0	0	0	
Gladioferans	0	0	14	1,760	40	20,110	11	200	(*d*)
Pseudodiaptomus	0	0	0	0	0	0	100	75,938	
Temora	67	2,184	42	1,163	0	0	0	0	
Acartia (*e*)	100	9,424	57	1,650	20	120	11	390	
Sulcanus	16	120	28	602	80	1,005,284	22	5,400	
Cyclopoida									
Oithona	67	2,322	57	5,051	20	2,344	100	1,423,856	
Mesocyclops	0	0	0	0	20	200	22	480	(*f*)
Oncoea	16	92	0	0	0	0	11	150	
Corycoeus (*g*)	16	120	0	0	0	0	0	0	
Corycella	0	0	0	0	0	0	0	0	
Harpacticoida									
Euterpina	16	120	0	0	0	0	0	0	
Microsetella	0	0	57	14,149	0	0	0	0	

APPENDIX VIII (*continued*)

	Station 1		Station 6		Station 11		Station 15		
	Frequency (%)	Total	Frequency (%)	Total	Frequency (%)	Total	Frequency (%)	Total	
Copepod Nauplii	82	2,892	57	4,509	80	7,907	33	1,780	
Copepodites (*h*)	100	2,664	57	15,111	40	256	33	3,902	
Cirripede Nauplii	82	770	43	2,520	20	400	0	0	
Cirripede Cypris	50	372	0	0	0	0	0	0	
Malacostraca									
Peracarida									
Mysidacea									
Rhophalophthalmus	0	0	0	0	0	0	11	9	
Larva 1	0	0	0	0	20	3,720	0	0	
Larva 2	0	0	0	0	0	0	11	1,380	
Eucarida									
Euphausiacea									
Nyctiphanes adult	16	79	0	0	0	0	0	0	
Nyctiphanes larvae (*i*)	16	150	0	0	0	0	0	0	
Decapoda									
Lucifer adult	0	0	0	0	0	0	0	0	
Lucifer larvae	16	37	0	0	0	0	0	0	
Acetes larvae	16	40	0	0	0	0	0	0	
Trupea (*k*)	33	80	14	50	0	0	0	0	
Brachyuran larvae	100	1,227	57	1,678	20	48	33	2,835	
Polychaete larvae	16	24	14	105	0	0	0	0	
Nematode larvae	16	328	0	0	0	0	0	0	
Lamellibranch larvae	50	1,568	43	2,840	20	664	0	0	
Gastropod larvae	82	4,696	57	1,724	60	1,104	11	200	
Larvacea	50	540	0	0	0	0	0	0	
Ascidiacea	16	138	0	0	0	0	0	0	
Thaliacea	0	0	0	0	0	0	0	0	
Fish larvae	0	0	0	0	0	0	45	2,600	(*l*)
Fish eggs									
Long	33	364	0	0	0	0	0	0	
Round (*m*)	33	584	0	0	0	0	0	0	

Total = number of organisms counted in all 15 mm. N70 surface hauls.

Frequency = percentage occurrence of organisms in all counts. The number of tow nettings and hence number of counts is not constant for all stations.

Groups (*a*) and (*b*) demonstrate the distribution of marine and freshwater cladocerans, with *Podon* as the chief constituent in the former and *Bosmina* in the latter. Amongst the calanoid copepods, the dominance of the marine end of the system by *Paracalanus* and of the freshwater end by *Pseudodioptomus* in large numbers is particularly apparent (Groups (*c*) and (*d*)). The range of genera in Group (*c*) compared with (*d*) is possibly due to the highly selective nature of the latter environment. The comparative barrenness of the gradient zone at Stations 6 and 11 in most of these cladoceran and copepod organisms is very apparent. The high and persistent population of *Sulcanus* at Station 11 is an important exception.

Amongst the larvae of the plankonic copepods a fairly even distribution of larval forms occurs Group (*h*)). The maximum concentration of larval forms of the burrowing invertebrates of the marine end of the system is normally in the same zone at Station 1, Group (*k*). However, brachyuran and gastropod larvae persist in all zones.

These plankton data suggest that there is some planktological significance in the hydrologically established zones in the Hawkesbury River. A similar investigation in marine, tidal, and freshwater dominated estuarine systems should yield particularly valuable information.

The need for investigation of the physiology of adaptation of estuarine plankton to their environment is also apparent. Recent papers by Panikkar (1941) and by Gross (1940) are important in this connection.

APPENDIX IX

MICROPLANKTON, SHELL POINT

In 1949, a pumping unit for the collection of plankton at Shell Point, George's River, was put into operation. Although such a collecting technique is considered inaccurate for estimation of macroplankton, the protozoa, dinoflagellates, and diatoms caught by this technique on the finest sieve should be quantitatively representative of these microplankton forms.

TABLE 14

TINTINNID SP. (TOTAL COUNT PER 50 GALLONS) AT JETTY PLATFORM, SHELL POINT

Date	Tide	Time	Depth	Count	Interval
7. i.1949	Low	6 a.m.	Bottom	1,730	
24. i.1949	High	6 p.m.	Bottom	300	
25. i.1949	Low	12.15 p.m.	Surface	20	29 Days
5. ii.1949	Low	6.40 a.m.	Surface	20,404	
12. ii.1949	High	8.40 p.m.	Bottom	2,170	
12. ii.1949	Low	2 p.m.	Bottom	710	
10. iii.1949	Low	10.30 p.m.	Bottom	120	57 Days
19. iii.1949	High	0.15 a.m.	Surface	0	
3. iv.1949	High	11 a.m.	Surface	3,366	
16. iv.1949	High	10.45 a.m.	Bottom	3,060	
22. iv.1949	High	5.40 p.m.	Surface	131	
30. iv.1949	High	9.34 a.m.	Surface	102	
30. iv.1949	High	9.34 a.m.	Bottom	1,224	
6. v.1949	High	3.09 p.m.	Surface	125	
7. v.1949	Low	9.56 a.m.	Surface	0	40 Days
13. v.1949	High	8.50 a.m.	Surface	33	
31. v.1949	High	10.49 p.m.	Surface	0	
17. vii.1949	High	1.29 p.m.	Surface	702	65 Days
16.viii.1949	High	1.23 p.m.	Surface	12,802	

The numbers of tintinnids filtered from 50 gallons of sea water, for each pumping carried out during the period January 7 to August 16, 1949, are listed in Table 14. It seems fairly clear that in the period covered by this table, the development of four swarms of tintinnids occurred. Whilst the data are insufficient to provide convincing evidence, there is some indication that these swarms originated in the bottom waters and hence could have been stimulated by conditions at mud surface.

The role played by the intertidal muds in the development and maintenance of such microplankton forms is of great economic importance in oyster nutrition, and should provide a fruitful field for the marine physiologist and ecologist. The collection and counting of data in this appendix were carried out by Mr. E. A. Bennett, of the Division of Fisheries, C.S.I.R.O.

APPENDIX X

ADJUSTMENT OF SURFACE OBSERVATIONS FOR TIDAL DISPLACEMENT IN THE GEORGE'S RIVER SYSTEM

To carry out this adjustment it is necessary to have a continuous record of the tidal rise and fall, preferably at a point within the system representative of average conditions. Although not ideal, Shell Point was used at this observation point. Secondly, it is necessary to repeat the sampling at a point within the gradient zone, at an interval less than the normal time of approximately six hours required by a semi-diurnal tide to vary from a low to a high water level.

The station at Como Bridge (No. 9) was selected for this purpose. The following table gives the calculation of these tidal adjustment values for a survey of the George's River on October 19, 1943, when a rather steep chlorinity gradient was in evidence. The displacements listed are in inches and represent the measured or calculated corrections to be applied to a standard longitudinal plotting of the chlorinity data.

Time of first sampling at Como = 8.13 a.m.
Time of second sampling at Como = 12.43 p.m.
Displacement interval = 4½ hours
Displacement of initial water mass in above interval = 1.1 units on plotting
Total calculated displacement in half tide cycle = 1.46 units on plotting

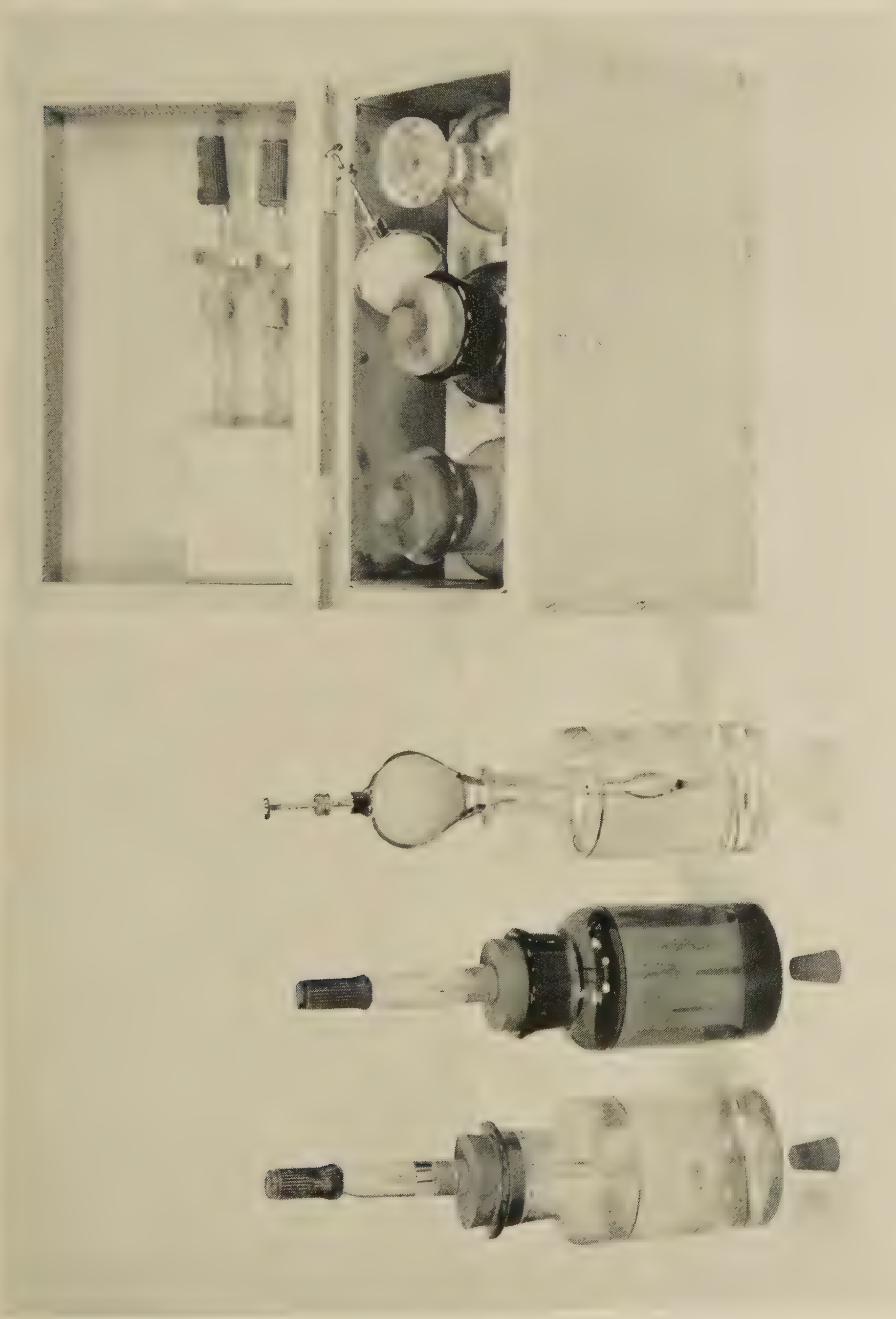
In the next table the calculation of the displacement correction for all stations on the survey is given, together with an estimation, in the last column, of the error in Cl°/00 introduced by the neglect of the displacement correction.

TABLE 15

TIDAL DISPLACEMENT CORRECTIONS

Station	Time Sampling	Time L.W.	Interval to L.W.	Calculated Displacement Correction (in.)	Cl°/00 Error
Tom Ugly's Bridge	1.15 p.m.	7 a.m.	5.75 hr.	1.46	3.2
Como Bridge	12.43 p.m.	7 a.m.	5.75 hr.	1.46	2.5
Lugarno	8.45 a.m.	7 a.m.	1.75 hr.	0.43	1.5
Salt Pan Creek	9.15 a.m.	7 a.m.	2.25 hr.	0.55	2.2
Picnic Point	9.35 a.m.	7 a.m.	2.5 hr.	0.61	0.5
Williams Creek	10.05 a.m.	7 a.m.	3 hr.	0.73	0
Milperra	10.30 a.m.	7 a.m.	3.5 hr.	0.86	0

As can be seen from the figures in the last column, the differences between the original and the tidal adjusted chlorinity values were of significant magnitude, and in considering the distribution of hydrological properties for any particular survey, such adjustment should be made. However, if mean conditions over a number of years are being considered, as in the present paper, the error involved in neglecting such displacements in longitudinal plottings becomes insignificant.



Pipettes for the delivery, and the lead-lined box for the stowage and transport, of oxygen reagents.

THE NEW SOUTH WALES TIGER FLATHEAD, *NEOPLATYCEPHALUS MACRODON* (OGILBY)*

II. THE AGE COMPOSITION OF THE COMMERCIAL CATCH, OVERFISHING OF THE STOCKS, AND SUGGESTED CONSERVATION

By The Late W. S. Fairbridge*

(*Manuscript received September* 11, 1950)

Summary

The commercial flathead catch is analysed into its component age-groups. The results are expressed in numbers and weight of each age-group caught in each month. The results indicate an absence of natural fluctuations in abundance of the year-groups during the series of years covered.

The post-war decline in the catch of flathead is discussed in the light of this analysis. The catch has fallen from 5,700,000 lb. in 1944-45 to 2,100,000 lb. in 1948-49. The catch of flathead for a period between the wars is estimated at over 10,000,000 lb. per year. The stock of flathead has thus shown a failure to recover during the war-time rest, as well as a sudden fall with the inception of heavy fishing of recent years.

Possible reasons for these changes in the flathead stock are discussed. It is suggested that the numbers of recruits are limited by the numbers of spawning adults.

The results obtained from this work are fuller, but in entire agreement with those of the earlier paper on the trawlfishery as a whole. The adoption of conservation measures is urged. The trawlfishery is now dependent on two hitherto discarded species of poorer quality than the flathead, and the better of these is already showing a reduced catch per unit effort of fishing. The most important conservation measure is that suggested in the earlier paper—a reduction of the fleet to the equivalent of 13 trawlers. It is regarded as probable that if this step is not taken, the annual trawlfish catch will continue to decline. Closure of the Botany fishing ground is suggested as a further, but not an alternative, measure.

I. Age Composition of the Commercial Catch of Flathead

The first part of this study discussed the biology of the species and the method and data of age determination. In this paper there are frequent references to Part I and for the sake of uniformity they are quoted in the following way: (Fairbridge 1951, Section ...).

The technique of age determination from the otoliths was previously described and tested (Fairbridge 1951, Section III). These results are now applied to the commercial stocks.

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* Before his death in May 1950, Wolfe Fairbridge studied extensively the trawlfishery of the east Australian coast. He concentrated his attention particularly on the tiger flathead (*Neoplatycephalus macrodon*) and prepared a paper summarizing the whole of his results. In the final editing of the paper, which was done after the author's death, it was divided into two parts. Part I, dealing with the biology of the species and the method of age determination, appeared in Vol. 2 No. 2 of this Journal.

(*a*) *Method of Calculating the Age Composition*

The determination of the age composition of the commercial catch of many fish species is now a routine of fisheries research. The essential data for this work must comprise the figures for the total catch of the species and the age composition of a representative or random subsample of the catch. The precise manner in which the two groups of data are collected and expressed depends on the exigencies peculiar to the individual fishery. The collection of total catch statistics, in particular, is usually outside the duties of the research worker and he must accept them as provided by the responsible authorities. No one system developed to suit a particular fishery or species can be blindly applied to another.

When the flathead programme was being planned, Hodgson's (1939) paper seemed useful as an initial guide to follow. The sampling technique was therefore based on his for the herring. The flathead sampling programme is detailed in Part I (Fairbridge 1951, Section I (*a*)). The otolith samples were usually allowed to accumulate for six months or so and are then worked on together. The labour of "reading" the samples is not by any means excessive.

It is clear that, though there are figures available for the catch by the Danish seiners by areas, it is quite impracticable, owing to sampling difficulties, to calculate the age composition of the catch from each area monthly. Alternatively, it would perhaps be possible to arrive at the yearly age composition of the catch of each area separately, by obtaining an average for the year of the length-age relationship in that area. However, it is evident from the work on differences of growth rate between areas (Fairbridge 1951, Section III (*c*) (ii)) and differences in length distribution between areas (Fairbridge 1951, Section II (*c*) and Fig. 8) that no great errors will be involved if the differences between areas are ignored. The results of the work on raciation (Fairbridge 1951, Section II (*c*)) indicate a genetically homogeneous stock. Only the far northern (Newcastle-Port Stephens) samples show important differences from the others in growth rate and length frequency distribution, and the catch from this area is small. Moreover, no information as to area of catch is available for much of the Danish seiners' catch and all the trawler catch is from unknown areas.

There is a rather consistent and marked difference between the length frequency distribution of the catch by the trawlers and the Danish seiners. The trawlers catch a higher proportion of large fish. This is shown incidentally by Figure 8 in Part I (Fairbridge 1951, Section II) and is noticeable throughout all the tables of length frequencies. The reason, no doubt, is that the otter trawl is a larger, faster-moving gear than the Danish seine and presumably a smaller proportion of large fish would escape it; it is also probably true that the Danish seiners, working more inshore where the young flathead concentrate during their first two years of life, would be fishing a population of a smaller average size than the trawlers. Because of this consistent difference, and because of a good deal of disproportion in the monthly sampling, it is best to treat the catch by the trawlers and the catch by the Danish seiners separately.

Following Hodgson, but with some modifications, the data have been dealt with as follows: length frequency tables were drawn up for each month, with the trawler-caught samples separated from those of the Danish seiners. From the otolith "readings" a table was drawn up for each month showing the length-age distribution of the otolith samples; the trawler-caught samples in this case were not divided from the others because there were but small differences in length-age distribution between the sets of samples, and to divide the age samples would be to reduce the numbers too greatly. Another table was next constructed for each month and for the trawlers and Danish seiners separately, in which the frequencies at each cm.-group were divided into their age-groups by simple proportion from the length-age table. The mean weight (oz.) of each cm.-group was then entered in this third table; these weights were obtained from the market weighings in a manner to be described later. Next, the frequencies in each age-group were multiplied across by the appropriate weight (in oz.) and these products summed for each age-group (*d*), and the sums of these obtained to give a figure for the month (*b*) but again keeping the trawlers and Danish seiners separate. The actual catches in that month by the two types of gear were obtained from the State Fisheries' statistics and converted to oz. (*a*). This figure was divided by the sum of the total calculated weight of the samples for the month ($a/b = c$) and the total calculated weight of each age-group (*d*) was multiplied by this figure (*c*) to give the actual calculated weight in oz. of flathead of each age-group caught by each type of gear in the month ($d \times c = e$ oz.). These values (*e*) were divided by the average weight of the appropriate age-group to give the actual calculated number of flathead of each age-group caught by each type of gear in the month. By summing the two sets of figures (trawlers and Danish seiners), the total for the month was obtained; and by summing the months, the total for the year was obtained.

This treatment gives a manner of expression of the age composition of the commercial catch as complete as could be wished for. Its limitations lie in the inaccuracies due to the sampling, in the actual age "readings" from the otoliths, in the conversion from numbers to weights at each size-group, and finally in the gross statistics given for the total commercial catch.

These last have been dealt with in a former paper (Fairbridge 1948) but should be repeated here. The trawler catch is known with a good degree of accuracy. The managers of the trawler companies provide the State Fisheries Department with a monthly return stating the quantity of each species of fish taken in the month by each vessel. These figures can be checked by a market Inspector who is present at the unloading and sale of fish at the trawling companies' wharves. It is obligatory on the Danish seiner owners to provide a similar monthly return. It is known that a varying proportion of owners either do not provide returns, or understate their catches. A degree of check is possible from the State Fisheries annual figures of sales of tiger flathead through the Sydney Fishmarket and local depots; these showed that in 1947-48 somewhat more flathead was actually sold through these channels than was stated in monthly returns. These discrepancies, however, have not the same importance to the present discussion as to the problem of overfishing, for they presumably occur largely at random and would not affect the actual age composition study. It should be noted that the market samples do not provide a reliable estimate of the quantities or proportions in which undersized fish are actually caught. Large catches of such flathead would either be shovelled back into the sea, or disposed of locally.

The probable accuracy of the age "readings" has been dealt with in the preceding paper (Fairbridge 1951, Section III (*d*)). It is likely that errors may be of some magnitude in certain samples. But the above method of treatment involves the use of large numbers of length frequency measurements, which are direct and considered well representative of the catch of flathead. Large-scale changes in the age composition of the catch would be reflected in the length frequencies. The length frequencies are examined in Section I (*c*) and are found to be in general agreement with the results of the age determination work. Big changes are likely to be most marked in the younger age-groups, and in these groups the age determination technique is relatively certain.

As regards the conversion from numbers to weights, it had at first been intended to use the weighed samples directly to provide mean values at each cm.-group for the month and year to which they referred. This proved unsatisfactory in many months, owing to the low numbers sampled, and to the rather wide discrepancies between samples in the same month. When it became apparent that there were consistent changes with the seasons in the weight-length relationship but little difference in maximal and minimal values between years (Fairbridge 1951, Section II (*b*)), it was decided to lump the weighed samples of the three years, May 1946 to May 1949, and to derive mean values therefrom for each of the 12 months and to use these mean values in converting from numbers to weight.

This is obviously less satisfactory than the originally intended method, but probably causes smaller errors than the large sampling errors that would otherwise result. In any case, the seasonal differences in the weight-length relationship are small, not amounting to 15 per cent. for the most abundant size-groups. To obtain an estimate of the weight at each cm.-group, the logs of the mean values obtained from the samples were plotted for each month against the logs of the cm.-groups. A straight line, which approximately fitted the points, was then drawn with the aid of a transparent ruler. The advantage of drawing this line is that discrepancies between adjacent mean values are cancelled out, and readings may be taken by interpolation, or extrapolation beyond the range of the original data. The straight line of best fit might have been calculated, but the labour did not seem worth while in view of the approximations involved elsewhere in the method. Experiment showed that it would be subjectively impossible to draw two alternative lines for any one month varying by as much as half an oz. in the lower size-groups. This method gave apparently satisfactory lines from which to read off the weight at each cm.-group.

Approximations had to be made in obtaining some of the proportions from the length-age tables. The length frequency data often extended above or below the range of the corresponding otolith data, and in the higher size-groups the otolith data often became discontinuous. The ages in the lower size-groups could be approximated with accuracy from the general age-length knowledge acquired from the experimental trawling. The lower age-groups are fairly distinct and little error would be involved in these approximations, particularly since frequencies in these size-groups are low. The higher age-groups had to be dealt with more subjectively, the proportions being decided by comparison with the otolith data from adjacent months, or failing that, from the same months of other years. In any case the numbers involved in these higher cm.-groups are low and could hardly affect the general results.

Of the three and a half years dealt with in this analysis of length and age, one month was found to have too few otolith "readings" from which to obtain the proportions of the age-groups. In this case, the otolith "readings" of the adjacent months were summed and used. There was occasionally deficient data on the trawler catch; in these cases the samples were treated as a whole, without division into trawler and Danish seiner data.

Finally, it was found possible to treat some data from the year 1940-41 in a comparable manner. Adequate length frequencies (3,000-8,000 per month) are known for the period July-February of this year. But a total of only about 400 otoliths, comprising 14 samples, is available, and there are no figures showing the size of the flathead catch. The data were therefore treated in the following manner: the length frequencies were summed for the whole period and expressed as percentages; the 14 samples of age determinations were combined, and the proportions of the age-groups at each size-group determined for the period as a whole; the percentage length frequencies were then divided according to these proportions, giving an estimate of the proportionate make-up (size- and age-groups) of the catch. The length frequencies above 51 cm., which amounted to about 0.5 per cent. of the total, were omitted as there were no age determinations in these higher size-groups by which to interpret them. The VI-group must therefore be considered incomplete, and the VII-group should probably be represented.

(*b*) *Age Composition*

From the viewpoint of the practical understanding and control of the fishery, the chief purpose of this paper has been to analyse the catch in such a way that any natural population fluctuations will be revealed. It is required to know whether such fluctuations occur, what effect they might have on the fishery, and in particular, whether the recent spectacular decline in the flathead catch can be explained as a natural fluctuation. We are now in a position to make this analysis.

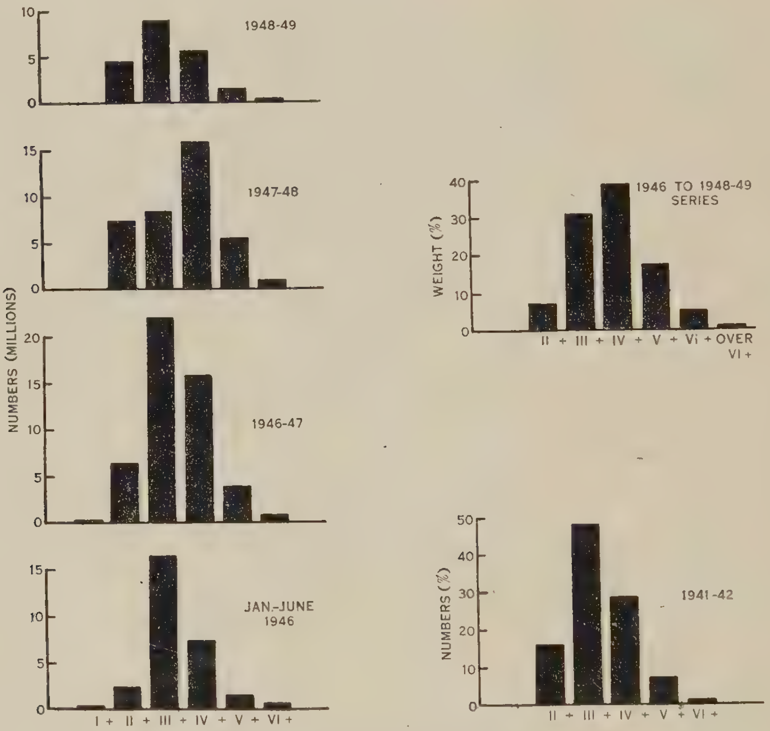

Fig. 1.—Age composition, by numbers, of the flathead catch; age-groups older than VI+ omitted. Also the age composition by weight of the series 1946 to 1948-49, and percentage age composition of the 1941-42 catch by numbers.

In Figure 1 the calculated numbers of flathead of each age-group taken in each year are shown as histograms. The 1946 (January-June) series represents only half a year; the histograms for that year are therefore only about half as high as they should be; there is also a slight bias, for, as will be shown later, the 1-, 2-, and perhaps 3-year fish tend to figure rather more prominently in the latter half of each year. The 1941-42 histograms do not refer to actual numbers of fish but only to the proportions between the age-groups; this year also is incomplete, and would show a slight bias toward the older age-groups. The outstanding feature shown by Figure 1 is the degree of constancy in the relative proportion of the age-groups from year to year. There is only one slightly aberrant year (1947-48) in the five.

Except in this year, the 3-year-old fish are the most numerous, with the 4-year-olds in second place, and the 2-year-olds next. The relative proportions by weight of the age-groups in the 1946 to 1948-49 series are also shown in Figure 1. Taken by weight, it is evident that, for the industry, the 3- and 4-year-old fish are of approximately equal importance, the 5-year-olds in next place, and the 2-year-olds relatively unimportant in spite of their numbers.

The aberrant year, 1947-48, shows a relatively poor catch of III-group fish. These fish are the 1944-45 year-class. It was in this year that the flathead catch, after the war-time rest, suddenly rose to a maximum, from which it has since declined (see Section II). This subject will be returned to below.

TABLE 1

PERCENTAGE REDUCTION IN NUMBERS BETWEEN ONE AGE-GROUP AND THE NEXT ABOVE IT

	IV+ to V+ (%)	V+ to VI+ (%)	VI+ to Over VI+ (%)	V+ to Over V+ (%)
1948-49	75	72	90	69
1947-48	66	81	80	74
1946-47	75	78	85	78
1946 (½ year)	77	77	89	78
1941-42	75	—	—	—
Average	73.6	77.0	86.0	74.8

Because of the short life of this species, the number of age-groups available for study of the annual mortality is limited. The III-group may not be used, as it is incompletely sampled by the fishing gear. At the VI-group and over, age identification from the otoliths becomes somewhat uncertain and subjective, and sample size is small.

It is therefore only in the IV-group that an exact estimate of annual mortality can be made. However, five years are available, and as a result of the regular level of recruitment the results are not erratic. In Table 1 the percentage reduction in numbers between one age-group and the next is given for various age-groups. The left-hand column represents the annual total mortality of the IV-group (i.e. the numbers of fish in the IV-group, minus the numbers in the V-group, expressed as a percentage of the IV-group).

Clearly, the annual mortality of the IV-group can be taken as of the order of 75 per cent. The second column in the table gives the mortality in the V-group. As mentioned above, there is room to doubt the exactness of these figures. However, a higher level of mortality is indicated in this age-group, and this result is so interesting that it requires further study.

In the third column of the table the reduction of the next higher age-group, the VI-group, is expressed by lumping together the numbers of VII+ and VIII+ fish. No monthly figures for the VIII+ fish can be given, because in no month were the calculated numbers greater than 500. No otolith has yet been seen in which an age higher than VIII+ is clearly indicated. The effect of lumping these two age-groups together would give the appearance of reducing the mortality of the VI-group. Yet the values given in the table are higher again than those for the V-group.

In the fourth column, the mortality of the V-group is recalculated by lumping together all the specimens that were older than V+. This is taking it as if the author were completely in error in his identifications of the VII- and VIII-groups, and as if these age-groups were, in fact, unrepresented in the catch. Even so, the average annual mortality rate of the V-group is higher than that of the IV-group. Now it is, in reality, most unlikely that there are no VII- and VIII-group fish in the catch. A small proportion of the otoliths is clearly marked with seven and eight annuli; and the growth curves of Figure 21 (Fairbridge 1951) unmistakably point to the existence of age-groups older than VI+, corresponding to the large fish of 55-60 cm. and over. Some at least of the "over V+" in the table must belong to higher age-groups than VI. Their presence would increase the real total annual mortality of the V-group flathead above the value given in the fourth column of the table, and raise it even higher above the level for the IV-group.

An increase in total mortality after the fifth winter is the conclusion that is unavoidable. Alternatively, it may be that there is a continuously increasing annual mortality rate from some earlier period. It is not possible to attribute this increased mortality to any unequal incidence of fishing. Figure 3 indicates an inability on the part of Danish seiners, as compared with the trawler, to catch the larger flathead. This effect would be expected to reduce the mortality of the older, larger specimens.

There seems no reason to doubt, then, that the flathead is a naturally short-lived species, and that the annual mortality rates given in Table 1 indicate either the onset of increasing natural mortality or the later stages of a steadily accelerating natural mortality rate. It was earlier suggested (Fairbridge 1951) that heavy natural mortality was occurring among the males from a point about half-way through their third summer, i.e. probably after their second spawning.

It is difficult to suggest a likely important cause of natural mortality in the adult fish, other than senility. It seems that, as with the Indiana bluegill sunfish (Ricker 1945) senility is taking an increasing toll of the adult stock at a comparatively early age. This question has important bearings on the failure of the flathead stock to recover from overfishing.

The seasonal influx to the catch and subsequent reduction of the various age-groups can also be studied from the age composition data.

Figure 2 is derived from that table. Here the catch (by numbers) per unit effort of three important year-groups is plotted month by month. This provides a measure of the actual abundance of the year-groups. The data refer only to Danish seiners' catch.

It is obvious from Figure 2 that for no age-group is there any particular season showing a marked influx. Recruitment into the catch seems to be a steady process. The I- and II-groups figure more towards the end of each year, presumably as a result of growth by the individuals. The same is probably true, to a slight extent, of the III-group, since the smallest of these in July of each year are able to escape through the meshes of the codend.

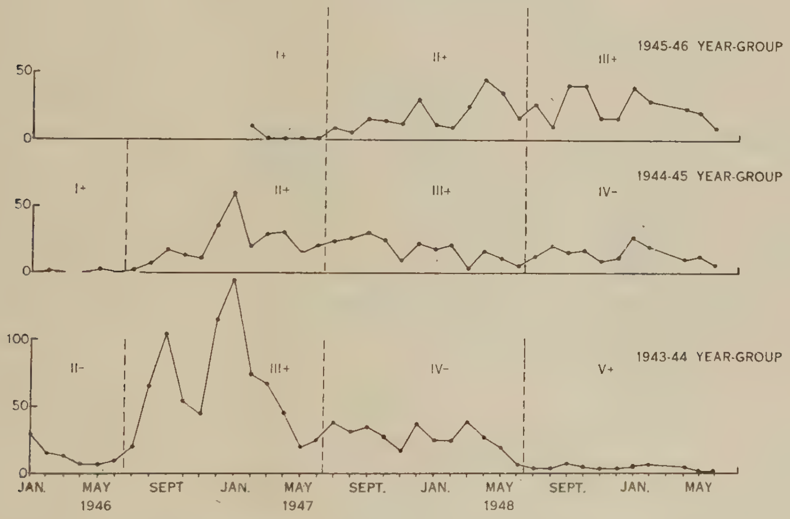

Fig. 2.—Number of flathead of three year-groups caught per unit effort by the Danish seiners.

Most of the age-groups show two broad maxima in the year, about September and about January. It should be remembered that the III-group are largely mature males, and the IV-group largely mature females. As only the largest of the II-group are caught, these too would mostly be mature or maturing males. The maxima in January are no doubt a reflection of the spawning concentrations. The subsequent minima are caused by the depletion of the year-group by fishing and scattering of the individuals. The author is unable to make any confident suggestion to explain the maxima in September, or the subsequent minima. This figure should be compared with Figure 9 (Fairbridge 1951) showing the seasonal catch of flathead in the different localities.

Figure 2 also gives a very good idea of the relative gross abundance of the year-groups; in particular, the lower numbers of the two year-groups following that of 1943-44.

(*c*) *Changes in Size Composition*

Turning now to the changes in the size composition of the flathead catch resulting from the war-time suspension and the subsequent heavy fishing, in Figure 3 the data have been treated similarly to that in Figure 8 (Fairbridge 1951); a total, or mean percentage length frequency curve was calculated for the four complete years 1945-46 to 1948-49, and from this mean the differences (plus or minus) of the percentage length frequencies in the individual years were calculated. It has been possible to represent 1945-46 fully; 1937-38 is represented by the months January-June only, 1938-39 by a total of five months, 1941-42 by ten months, and 1944-45 by the months August-October. The length frequency samples derived from the Danish seiners have been separated from those of the trawlers.

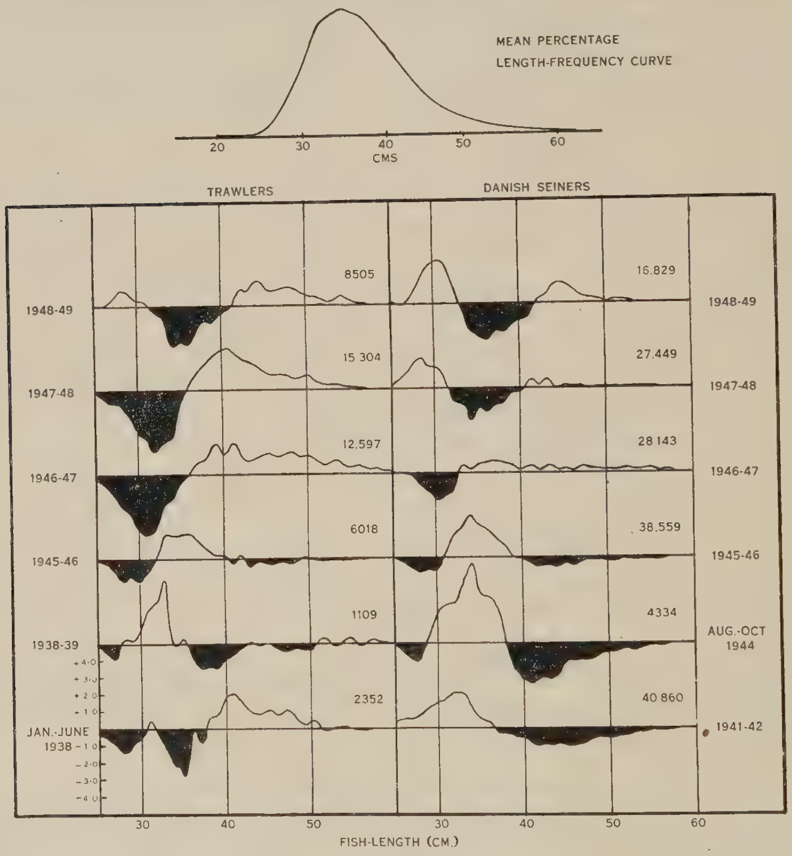

Fig. 3.—Differences (negative shaded, positive white) of the flathead percentage length frequency curves for various years from the mean percentage length frequency curve for 1945-46 to 1948-49. The numbers of specimens making up the curves are indicated on the right of each.

In interpreting the changes, we must anticipate to some extent Section II. The reader is referred, in particular, to Figure 5 and Table 3. Briefly, the position is that before the war the fishing intensity was relatively heavy, and was increasing as a result of the growing fleet of Danish seiners. The first year that saw a serious drop in the fishing intensity and in the catch was 1940-41, although the catch was not really low. The following year was similar. In 1942-43 and the following year, the catch and the fishing intensity were virtually nil. The subsequent years saw a rapidly increasing fleet of Danish seiners, and later of trawlers, and a very rapid increase in the catch to record size, with a subsequent drop. In interpreting the curves in Figure 3, it must be remembered that the trawlers tend to catch more large fish and fewer small fish than the Danish seiners; allowing for this, the two series in Figure 3 are in good agreement.

The earliest year shows the condition in a relatively lightly fished stock, namely, few small fish and large numbers of large fish. The following year (1938-39) shows that this condition had changed, presumably as the effect of increased fishing. The effects of continued and intensive fishing show in 1941-42; evidently the comparative relaxation of fishing in this and the previous year had not been sufficient for large fish to accumulate. What is now of the greatest interest is that the samples of 1944 and the following year, 1945-46, show little change in this condition. It is not until the three later years that large fish show up in excess in the catches (largely, of course, in the trawler catches). Progressively, too, in these years, the catch of the very smallest size-groups —those below legal length—is increasing.

It would be most desirable to have some length frequencies from years even earlier. Unfortunately the manner of presentation in Colefax (1934) makes comparison with his data for 1930 very difficult. In that paper only the modes of the various samples are indicated. There is, however, enough information to show that modes above 40 cm. were common (compare the mean length frequency curve for the post-war period in Fig. 3). Even setting aside the mode he found at 54 cm. (which refers only to fish from the Newcastle area), his Figure 9 seems to indicate that the mode at 42 cm. was the major mode of the whole series. The maximum size of the flathead does not seem to have been significantly larger then than it is today.

II. OVERFISHING OF THE STOCKS

(*a*) *The History of the Fishery*

Dannevig (1915*a*, 1915*b*) described briefly the nature of the bottom on the New South Wales trawling grounds, and Colefax (1934) described the fishery as it was in 1930, and included a plate showing the main trawling areas. Fairbridge (1948) gave an account of the history of the fishery from its inception in 1915 up to the year 1946-47 as revealed in the catch statistics. There have been a number of changes in the fishery since Colefax's work, and it will perhaps be found convenient to repeat here briefly the main features of the fishery.

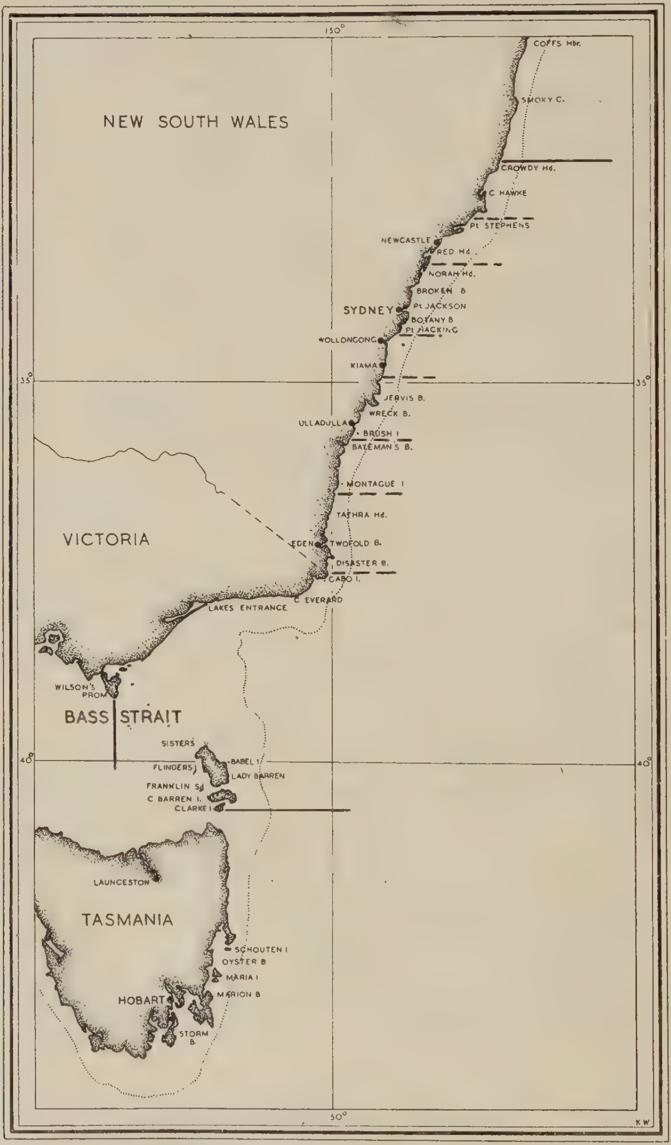

Fig. 4.—Area of the eastern Australian trawlfishery, approximate limit of the continental shelf, and places mentioned in the text. The heavy black lines indicate the approximate limits of the main flathead fishery; the broken horizontal lines indicate the limits of the areas mentioned in the text.

After the excellent exploratory work by Dannevig (Commonwealth of Australia 1909, 1910; Dannevig 1913) from 1909 till the loss of the

"Endeavour" with her crew and much of Dannevig's unpublished material in December 1914, the fishery was begun on the initiative of the New South Wales Government in 1915. Towards the end of 1922 the State withdrew from the enterprise (Herlihy 1927), and the fleet of seven trawlers passed into the hands of private operators. Fishing recommenced in 1923 and by 1929 the fleet was built up to 17 trawlers. That year saw a peak of production. But the rate of catch had already been falling for some years, and there was a decline of the total catch from 15,000,000 lb. in 1929 to 9,000,000 lb. in 1934; the decline was caused partly by the rate of catch continuing to fall and partly by a steady decline in the number of trawlers to 13 (see Fig. 5).

The grounds fished up till about 1930 had been those from Crowdy Head to Gabo Island. These consist variously of mud and sand, separated by unworkable areas of foul ground, and are situated between about 30 or 40 fathoms and the edge of the shelf. The shelf on this coast falls off very steeply at about 90 or 100 fathoms and is quite unworkable with the otter trawl. A significant feature of the early years was the "Botany glut"—an annual concentration of spawning flathead on the Botany ground within a few miles of Sydney. The year 1924 or 1925 saw the last of these gluts.

After about 1930 the trawlers began to work extensively along the eastern edge of the Bass Strait shelf, where Dannevig had done much of his earliest work and had obtained some of his best results. The weather in Bass Strait and the distance from the home port, Sydney, are deterrents to fishing there. Nevertheless, the steam trawlers today confine their efforts almost solely to this area. South of Flinders Island the catches appear to fall off badly, and this may be taken as the effective southern limit of the trawling grounds.

Until 1936 the vessels were all typical small steam trawlers of 200-300 tons, mostly imported from the United Kingdom. Vigneron-Dahl gear had been introduced in 1925 or 1926. Sporadic efforts had been made from time to time with the Danish seine, a gear that had come into common use in New Zealand with the end of the first world war. The early attempts to use it on the New South Wales coast were unsuccessful, partly because of the strong currents met with as a rule and partly because of the relatively deep water in which pioneering efforts had to be made. There are few places on the New South Wales coast where gear of this sort can be used in less than 30 fathoms; the slope of the bottom is markedly steeper shorewards of this contour, and as a rule is obstructed by rocks and reefs; the beginner must, therefore, start operations under somewhat difficult conditions. But in 1937 several vessels began using this gear successfully. One of these early successes was in Tasmania, where there is little fish to be had by this method (Blackburn and Fairbridge 1946) but where conditions are less difficult. In all cases the so-called "flying-start" was used, that is, the dan-buoy is not anchored, and the vessel travels slowly ahead while the gear is being hauled in; this technique (which has been made illegal in some parts of the world) is necessary because of the current, which is inclined to drag the dan-buoy under if it is anchored, and by reason of the active character of the flathead, which escapes a slow-moving net.

The use of this gear increased rapidly after the first successes, and by the start of the second world war the Danish seiners were making a significant contribution to the catch.

Early in the second world war all but two of the trawlers were requisitioned for mine-sweeping; but the number of Danish seiners continued to rise till the outbreak of war with Japan. Most of them were then requisitioned; so that for two years, 1942-43 and 1943-44, there was little fishing. After that year, however, the number of Danish seiners increased until 1948-49, when it began to fall, probably as a result of poor fishing. Reintroduction of trawlers began in 1944-45 and their numbers rose to 11 in 1946-47.

The fleet today consists of 12 trawlers and a variable number of Danish seiners (Tables 2, 3, and 4). The trawlers are mostly the same vessels that have been fishing off the New South Wales coast since the 'twenties, but there have been some additions. The Danish seiners are vessels mostly about 45-50 ft. long, and powered with diesel motors; they operate in 30-40 fathoms, rarely up to 70 fathoms or more, and work mostly by day. The average depths worked by two trawlers in 1939 were 61 and 64 fathoms. The Danish seiners work from ports all along the coast from Port Stephens to Eden, and recently from Lakes Entrance, Victoria. They do not fish the eastern shelf of Bass Strait. The Bass Strait area was, in fact, thoroughly rested during the war, no fishing being done there from about 1940 to 1946.

The east Australian trawlfishery covers a continuous and somewhat uniform environment. Flathead is the dominant trawlfish throughout, and, in fact, the trawlfishery may be said to be limited by the distribution of the flathead. The limits of its regular occurrence are Crowdy Head to the north, Wilson's Promontory to the west, and Storm Bay, Tasmania to the south. Eden is the approximate geographic centre of this range, and is certainly one of the richest areas for this species. The general fauna that comes up in the trawl strikes the observer as very uniform over most of this area; such changes as do occur, occur gradually, except that in the small extension of the fishery in Tasmanian waters there come a few obvious changes. Temperature is perhaps the factor that changes most over the range (Fairbridge 1951, Fig. 13).

The only legal restriction on the flathead catch is a size limit of 13 in. (33 cm.) in New South Wales. Fish below this size that are sent to the Sydney Fishmarket (and virtually the whole catch goes through that market) are liable to be seized. As the length frequency data will show, this regulation is interpreted very liberally, for it is realized that the great bulk of the small flathead are dead when they come up in the trawl. The law can act usefully only by deterring fishermen from fishing concentrations of undersized fish. As a rule, a consignment is seized only if a very high proportion is undersized. The codend mesh universally used in the trawlers is 3 in., double twine; in the Danish seine it is usually 3 in., single twine, but more recently codends of a mesh as small as 2 in. have been used, more particularly off Lakes Entrance where a small mesh is necessary to retain the whiting (*Sillago ciliata*).

(*b*) *History of the Trawlfish Catch*

Statistics of the New South Wales trawlfishery (all species) are available from its very inception in 1915, and were discussed previously as a whole (Fairbridge 1948). Little information is available on the catch of the individual species, but the gross data are sufficiently full to draw some definite conclusions. It was shown in the above paper that the fishing intensity in 1946-47 was greater than it had ever been in the past, and reasons were given for believing that the trawlfish stocks would not stand indefinitely such heavy exploitation. Since that paper was written the fishing intensity has increased, and the total catch has fallen. The particular effects on the flathead stock will be examined here.

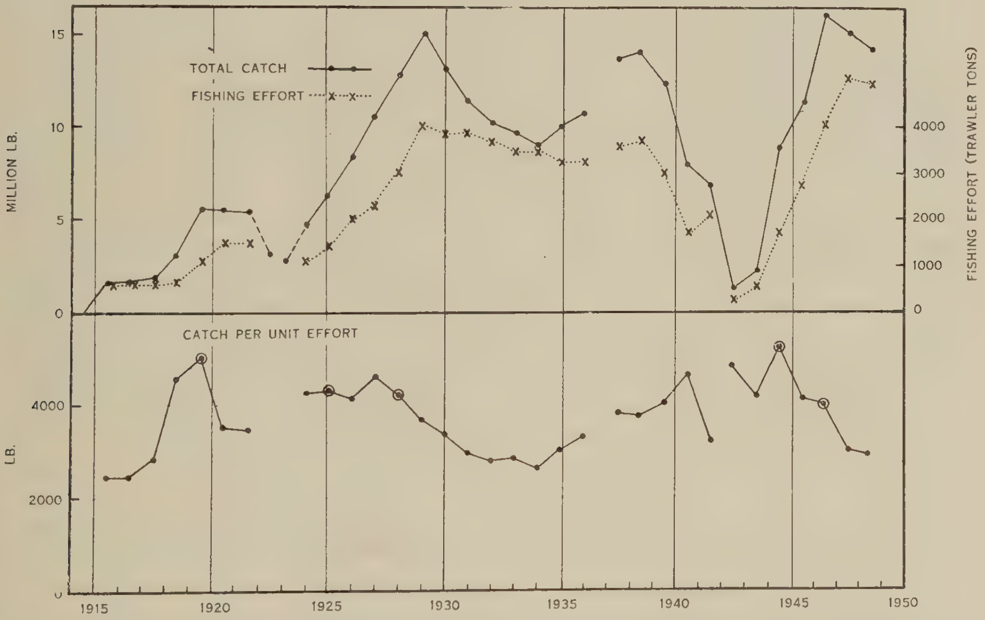

Fig. 5.—Total catch (all species) by the New South Wales trawlfishery since its inception, fishing effort (Danish seiners and trawlers combined) expressed in trawler-tons, and catch per unit of fishing effort.

Figure 5 has been brought up to 1949. It is presented here to show the broad history of the trawlfishery. A critical examination of the source and validity of the statistics has been given (Fairbridge 1948). In Figure 5 the total catch of all species is given by the unbroken top line. The fishing effort is somewhat crudely measured by the gross tonnage of trawlers operating in each year (see Hickling 1946; Fairbridge 1948 for the necessity to take into account the gross tonnage of the trawlers). The Danish seiners have been included in the total fishing effort by considering one of these vessels as equivalent to 30 trawler-tons. The lower unbroken line in Figure 5 gives the catch per unit fishing effort. This is simply the total catch divided by the fishing effort. Individual points must not be given too much weight, but it is believed that the general changes in level reflect the true state of things. Points marked by a circle are approximations made necessary by large numbers of trawlers entering or leaving the industry in a year.

The salient features of this figure may be summarized briefly. During the early years the catch per unit effort was high (for comparison with trawlfisheries overseas, it was of the order of 4-6 cwt. of flathead per hours' trawling). From 1927, when the catch was still rising, the catch per unit effort began to fall. In 1930 the catch itself was falling, in part as a result of the heavy fishing, and the catch per unit effort continued to fall till about 1934. But by then the fishing intensity had fallen, the stocks appear to have been recovering; the catch and catch per unit effort began to rise. From 1937 the fishing intensity increased as a result of the influx of Danish seiners. Before they could have much obvious effect, the trawlers were being requisitioned for the war. During the war, catch and fishing intensity were low and the rate of catch rose to that of the early years. With the end of the war, the fishing intensity increased to a height hitherto untouched; the catch also rose to a record, but began to decrease very soon; and the catch per unit effort fell to the 1934 level.

(c) *The Flathead Catch of Recent Years*

The above history refers to the total catch of mixed species. As will be shown later, this consisted of 80-90 per cent. flathead in the early years, but the proportion has fallen greatly since.

The catch and rate of catch of the three major species will now be examined for the years after 1941-42; later, some further data will be used to compare the catch of flathead today with the catch at several periods in the past.

Table 2 gives the catch and rate of catch of flathead, of the two other main species, and of total fish by the Danish seine fleet in New South Wales. The data were obtained from the fishermen's monthly returns. It is probable that the catches shown on these returns, particularly in 1945-46 and 1946-47, have been understated by perhaps as much as a quarter. The calculated average number of vessels working in each month was obtained principally from lists supplied by the fisheries inspectors, showing the names of the Danish seiners operating from each port in each month. This method of expressing the number of vessels is necessary because Danish seiners are constantly moving in and out of the fishery, changing hands or lying idle, and the number of licenses issued in each year gives no true picture of the fishing intensity.

TABLE 2

CATCH AND RATE OF CATCH OF THE DANISH SEINERS

Year	Catch (millions of lb.)				Rate of Catch (lb. per vessel per month)				Calculated Average No. of Vessels Working in Each Month
	Flathead	Morwong	Nannygai	Total Fish	Flathead	Morwong	Nannygai	Tctal Fish	
1942-43	0.02	—	—	0.04	1,571	—	—	2,817	1
1943-44	0.7	0.01	—	1.2	5,968	115	1	9,800	10
1944-45	5.0	0.3	0.02	7.1	12,189	643	59	17,414	36
1945-46	4.0	0.4	0.05	7.2	6,771	661	91	12,158	57
1946-47	3.1	0.5	0.1	7.6	4,155	653	160	10,253	67
1947-48	1.8	0.4	0.2	5.1	2,632	602	326	7,438	75
1948-49	1.2	0.5	0.5	4.1	2,513	1,011	966	8,518	58

Similarly, Table 3 gives the catch and rate of catch by the New South Wales trawler fleet. These figures are believed to be substantially accurate. The trawler-ton-months are obtained by summing the gross tonnage of the trawlers operating in each month of the year.

TABLE 3

CATCH AND RATE OF CATCH OF THE TRAWLERS

Year	Catch (millions of lb.)				Rate of Catch (lb. per trawler-ton-month)				No. of Trawlers	Trawler-Ton-Months
	Flathead	Morwong	Nannygai	Total Fish	Flathead	Morwong	Nannygai	Total Fish		
1942-43	0.5	0.02	0.1	1.3	157	6	40	380	1	3,290
1943-44	0.5	—	0.05	1.1	237	1	25	505	1	2,133
1944-45	0.7	0.3	0.08	1.9	95	36	11	251	1-4	7,393
1945-46	1.2	1.6	1.8	4.2	92	119	56	312	4-5	13,410
1946-47	1.9	3.4	1.8	8.9	74	134	72	333	6-11	25,801
1947-48	1.9	3.5	3.2	10.0	60	109	100	309	12	32,301
1948-49	0.9	2.6	5.1	10.1	25	71	141	282	12	35,881

Finally, the fish caught by the two fleets are given in Table 4. To obtain the total fishing effort, the average numbers of seiners shown above as fishing in each month were multiplied by 30 (to bring them to trawler-tons) and again by 12 (to bring them to trawler-ton-months) and added to the trawlers' fishing effort, also shown above.

Taking first the catch by the fleets combined, it is clear that until 1947-48 the fishing effort increased rapidly. In that year the total fish caught began to fall. The catch of flathead reached a peak of nearly 6,000,000 lb. in 1944-45 and has been declining since, in spite of increased fishing efforts.

TABLE 4

CATCH (MILLIONS OF LB.) BY THE DANISH SEINERS AND STEAM TRAWLERS COMBINED

Year	Flathead	Morwong	Nannygai	Total Fish	Total Fishing Effort (thousands of trawler-ton-months)
1942-43	0.5	0.02	0.1	1.3	4
1943-44	1.2	0.02	0.05	2.2	6
1944-45	5.7	0.5	0.1	8.9	20
1945-46	5.2	2.0	0.8	11.3	34
1946-47	5.0	3.9	2.0	16.2	50
1947-48	3.8	3.9	3.5	15.1	57
1948-49	2.1	3.0	5.5	14.2	57

On the other hand, the catches of morwong and nannygai have each in turn increased as the flathead catch decreased. This is an apparently conflicting situation for which there is an obvious answer. The relative values of the three species can be expressed as their fixed wholesale prices (1950), namely flathead 1/1 per lb.; morwong 10d. per lb.; nannygai 8d. per lb. Prior to the second world war the latter two species were largely discarded. With the decreasing availability of the flathead, the fishing boats have had to make up their catches with the poorer-priced species. Tables 2 and 3 show that this action was taken almost exclusively by the trawlers. The species are not readily available to the Danish seiners. The total catch taken by the trawlers has therefore gone on rising in quantity (though not proportionately in value) with the increasing effort, while the catch by the Danish seiners has been falling since 1944-45. The catch of morwong is now declining.

The catch of flathead and the rate of catch of the Danish seiners reached a maximum in 1944-45. Before this, the low rates of catch reflect inefficiency in the industry, which was using makeshift gear and boats, and not the size of the flathead stocks. By 1944-45, however, efficiency had greatly improved and the industry was working on accumulated stock that had a chance to build up during the two or three years' rest provided by the war. After this one year of good fishing, the catch and rate of catch of flathead (and the figures must be believed, since the 1944-45 figure is, if anything, an underestimate) had fallen to one-fifth of the peak.

The decline in the rate of catch of flathead by the trawlers has been equally startling. The catch did not begin to decline till 1948-49. In fact, however, the rate of catch had been falling since 1943-44, and is today little more than a tenth of that level, or one-quarter of the 1944-45 level.

The wide discrepancy between the 1942-43 and 1943-44 rates of catch by the trawlers is no doubt in part due to these figures being derived from a single vessel. The author has no explanation to offer for the very low rate of catch shown by Figure 5 for the year 1941-42, except to repeat that the units of fishing effort used in that figure are crude and too much weight must not be given to individual values.

Discrepancies in the decline of the catch per unit effort by the trawlers and Danish seiners undoubtedly reflect the condition of the different portions of the stock of flathead on which the two fleets fish. Whereas before the advent of the Danish seiners the trawlers fished along the whole coastline and in eastern Bass Strait, when the trawlers returned to New South Wales waters after the war they found the coastal grounds pre-empted by the Danish seiners to such an extent, and the stock of flathead there so depleted, that they have since fished almost exclusively the waters of eastern Bass Strait, which are unavailable to the Danish seiners. The Danish seiners, on the other hand, being unable to augment their catches with morwong and nannygai, have been much harder hit by the depletion of the flathead. The fall in numbers of Danish seiners bears evidence of this.

Depletion of flathead has been beneficial in one way: the hitherto discarded, but perfectly wholesome species such as morwong, nannygai, and many other less common kinds are now landed and used by the public.

(*d*) *The Level of Catch in the Past*

So far, it has not been possible to say anything about the catch prior to 1942. It is obviously of the utmost importance to have some idea what the level was, and to compare it with the peak catch taken since the war and with today's depressed level. There are available some trawlers' logs for some of these early years that give the catch of flathead and of other species. The logs for the whole fleet are not available; hence the total catch of flathead cannot be obtained directly. But if we may assume that the proportion of flathead in the catches of these individual vessels is the same as the proportion in the catches of the whole fleet in those years, we may derive an approximate value for the total flathead catch.

Table 5 presents this data. The early logs fall into three groups. For ease of comparison, some of the columns of the table have been continued to 1949 from data contained in foregoing tables, making a fourth group. The table refers principally to trawlers; on the right-hand side the growth of the Danish seiner fleet is indicated, with their rates of catch expressed in the same units as those of the trawlers; these rates of catch must not be regarded as anything more than approximately comparable.

The astonishing fact is presented in this table that the catch of flathead was of the order of 12 or 13 million lb. at the peak of the fishery in 1929.

Even in 1937-38 it was 7,500,000 lb. Whereas, after several years of almost complete rest during the second world war the catch rose briefly to a mere 5,700,000 lb., and then fell to 2,100,000 lb. It has already been admitted that this figure of 5,700,000 lb. is probably an underestimate. But it is difficult to believe that it is wrong by much more than 1,000,000 lb. Even in 1933, the past year of poorest fishing (Fig. 5), the flathead catch was 6,300,000 lb.; and this in spite of previous heavy fishing.

TABLE 5

FLATHEAD CATCH 1918-19 TO 1948-49

	Trawler Catch Only					Rate of Flathead Catch by Danish Seiners (lb. per trawler-ton-month)
Year	Proportion of Flathead in the Catch (%)	No. of Vessels from which Proportion was Derived	Estimated Total Flathead Catch (millions of lb.)	Catch of Flathead per Trawler-Ton-Month	No. of Danish Seine Licences Issued	
1918-19	88	7				
1919-20	87	7				
1921-22	82	7				
1922-23	81	7				
1928	95	1	12.2	367*		
1929	87	1	13.1	295*		
1930	80	1	10.5	243		
1931	80	1	9.1	224		
1932	76	1	7.8	201		
1933	65	1	6.3	174		
1937-38	65	14	7.5	180	5	
1938-39	62	5	7.2	174	6	
1939-40	68	8	5.8	204	10	
1940-41	59	4	2.3	218	26	
1941-42	41	3	0.9	123	49	
			Actual Flathead Catch			
1942-43	41	1	0.5	157	19	52
1943-44	47	1	0.5	237	60	199
1944-45	38	1-4	0.7	95	97	406
1945-46	29	4-5	1.2	92	105	223
1946-47	22	6-11	1.9	74	123	138
1947-48	19	12	1.9	60	134	88
1948-49	9	12	0.9	25	110	84

* These figures have been approximated.

There seems to be no reason to question the validity of Table 5. Though the 1928-33 series is based on a single trawler, which might be strongly biased, a most important piece of confirmatory evidence is given by Colefax (1934), who states that the percentage of flathead in the catch of the ships of one of the trawling companies (not the one to which the above vessel belonged) in 1930 was 83. The corresponding figure in the table is 80 per cent.

The proportion of flathead in the catch appears to have diminished very steadily; the figures are not erratic. It would almost seem that the recent decrease in the flathead catch and the increase in the catch of other species is merely a continuation and acceleration of a long-established process. It is not suggested that the other species (morwong, nannygai, etc.) have become more common; enquiries among the trawler skippers with experience going back to the 1920's show that these poorer species were caught in the old days, but discarded. No doubt concentrations of these species were formerly avoided, but are now sought after; no natural increase in these species has made itself noticeable to the fishermen. In short, there can be no doubt that there has been a very serious diminution in the stock of flathead available to the fishery.

This reduction in stock has been of a markedly more permanent nature than usually results from overfishing. For two years (1942-43 and 1943-44) fishing intensity and total catch were virtually nil; for three years (1940-41, 1941-42, and 1944-45) fishing intensity was about half the level of the middle 1930's, and the catch was moderate or low by pre-war standards. Enough has been said in the section on the biology of the flathead to show that this rest was ample for the supplies of 1- and 2-year-old recruits to grow to maturity and spawn at least once, besides themselves reaching catchable size.

What happened was that in 1944-45, with less than half the pre-war fleet working, the catch of flathead rose to a level approaching (though still below) the pre-war level. In each of the following two years the fishing intensity almost doubled; but the flathead catch dropped in each case. In 1947-48, with the fishing intensity still increasing, the flathead catch fell more rapidly to half the level of 1937-38, and eventually to between a third and a quarter of this level. The failure of the New South Wales trawlfishery to make a more spectacular recovery than in fact happened has been commented upon (Fairbridge 1948). At that time, the full significance was not realized, since no distinction was being made between species. It now appears that it was the flathead, the main species, which failed to recover to the expected degree. The catch of each of the two secondary species increased from almost nil till it was greater than that of the flathead. If the catch of flathead were today at the pre-war level of about 7,000,000 lb., the total catch should now be of the order of 18,000,000 lb. (Fig. 5).

(*e*) *The Failure of the Flathead Stock to Recover*

Why did the flathead stock not show more recovery after the war-time rest? In the first place, it might be argued that there has been a natural adverse population fluctuation coinciding with the end of the war. It was to answer this sort of question that the study of the age composition of the catch was undertaken. It can now be answered fairly briefly, from reference to Figures 1 and 3. It appears that, of the five years for which the information is available, the catch has been extremely uniform as regards the proportion of the age-groups. Only 1947-48 shows any abnormality, and that is not of such a degree or persistent enough to account for the low post-war catches. It appears that the flathead is not subject to remarkably good and bad recruit years, such as those described by H. Thompson and Raitt (various papers) for the North Sea haddock.

Another possibility is open: that there has been a long-term natural fluctuation resulting simply in a general diminution of the flathead stock over a period of one or two decades. Such changes must be pure conjecture as yet, but cannot be ruled out. The author is inclined to attribute the failure of the flathead to recover to other factors.

The first of these is that the stock has perhaps been depleted to such an extent that the numbers of recruits entering the fishery are dependent on the numbers of spawning adults. Although the reverse of this condition is often claimed for sea fishes (Hjort 1914, p. 161), it is obviously a theoretical possibility in every stock. It would seem to be especially likely in a stock such as the present, where there is stable recruitment from year to year. Under these conditions, an apparently uniform number of eggs is shed each year into the sea (the number varying over the years, but not erratically) and a uniform proportion of these perishes as a result of adverse conditions, while a uniform proportion survives. A uniform *number* would survive only if the supply of fry was so great that the quantity of food became the limiting factor; we know, from extensive plankton netting with N100 and N200 Discovery type nets, that platycephalid larvae do not occur in vast numbers on the New South Wales coast; the protracted spawning of the flathead would also tend to prevent concentrations; nor (in the two years for which we have information) was there evidence of intensive crowding of the O-group flathead on the bottom (beyond this size, mortality is probably relatively slight). Therefore, if the number of eggs shed into the sea is altered, this will directly alter the subsequent numbers of larvae and surviving fry. The number of eggs would be altered by altering the number of adults.

With the haddock, the proportion of eggs and fry that perishes or survives is so erratic (whether the limiting factors be food or physical conditions) that the number of survivors in each year is virtually (though presumably not absolutely) independent of the original number of eggs or of the numbers of spawning adults. Raitt (1939) records recruit broods of the haddock 60 times scarcer in some years than others, and more recently a ratio of 200 : 1 has been found.

But where the number of recruits is dependent on the number of spawning adults, a depleted stock will probably take longer to build itself up when released from heavy fishing. What would happen during the "fallow" period may be expressed diagrammatically as below. It is necessary to assume that it takes (say) three years for the females to reach maturity and to spawn (this is so in the flathead and approximates to the position in the haddock).

Year 1	Year 2	Year 3	Year 4
Small spawning	Increased spawning	Large spawning	Large spawning

The first two spawnings would be of relatively small size, since they are dependent on the size of the recruit brood produced by a depleted stock. The spawning of the second year would be *somewhat* larger than the first, since the stock of fish maturing in that year for the first time would not have been subjected to any fishing (assuming that the female flathead spawns first at about a length of 34 cm. it would have been subject to fishing for about half a year before it spawns). The actual stock of mature (catchable) fish during these two years would not be particularly large, since each recruit brood was small. The increase in the catchable stock would be due to growth of the few old fish, and accumulation of these relatively sparse recruit broods. As will be mentioned below, the accumulation of large fish is of limited effect in a short-lived species like the flathead.

In the third year, however, the first of these small (but unfished) recruit broods would spawn for the first time, and it would be the recruit brood resulting from this spawning that would really be large. These fish would become catchable (say) two to three years later, i.e. not until 5 or 6 years after fishing eased. The next year-brood would be about the same size, and the one following might be even larger if other factors did not limit it.

On the other hand, in a fishery where good and bad recruit years tend to alternate (e.g. the haddock), there would probably be at least one moderate or good recruit year already developing at the time of the cessation of fishing. This would be reaching catchable size within the first two or three years of the "fallow" period. Good and bad recruit years would follow and each good year would virtually be as good as if the fishery had not previously been depleted (though with the haddock, Raitt (1939) points out that the average size of the recruit broods of this species too has been lower during the period of heavy depletion).

The above comparison is simplified, but serves to point the fundamental difference between the two kinds of condition. It is evident that a species in which the number of recruits is limited by the number of spawning adults is much more susceptible to heavy fishing, and takes longer to recover. We have no direct proof that this is the condition with the flathead, but if we postulate that it is, the hypothesis will be found to explain many problems of the flathead catch over the last decade.

With this in mind, and turning to Figures 3 and 5, it will be seen that there was very heavy fishing immediately before and during the first year of the war. The estimated flathead catch of 5,800,000 lb. in 1939-40 was, in fact, taken by a fleet very little smaller than normal. The combined rate of catch by both types of fishing vessel was falling from 1937-38 to 1939-40. According to the above hypothesis, we would not expect the catchable flathead stock to increase greatly until the third year after fishing was relaxed. Actually, fishing was not relaxed greatly until after 1940-41 and 1941-42, which saw catches only somewhat less than those of the middle 1930's. The length frequency curve for 1941-42 (Fig. 3) shows a great deficiency of large fish. With some relaxing in the fishing intensity, one would expect moderate numbers of large fish to begin to appear; this deficiency must, in part, be a reflection of the heavily fished condition of the stock prior to this year. In 1942-43 and the year following, the catch was practically nil. Yet again, in August-October 1944, there is a deficiency of large fish, and this deficiency persists into the following year when it is apparent in the catch of both trawlers and Danish seiners.

It is not until 1946-47 that a really large proportion of large fish is apparent. These fish are the 4-, 5-, and 6-group, and would have been spawned in 1940-41, 1941-42, and 1942-43. In other words, it is the recruit broods derived precisely from the years of lessened fishing that are at this stage appearing in the catch in unusually large numbers. These size-groups persist in the trawler catches and to a lesser degree in the Danish seiners' catches, up to 1948-49. Thus, the last abundant year-group is seen from Figure 3 to be (probably) that of 1943-44—the last year of reduced fishing. The largest catch of flathead was in 1944-45, and from then on the year-groups appear in the catches in deficient numbers. The increase in the proportion of undersized fish in the catch of the Danish seiners of late years is merely a reflection of poor fishing, and is expected.

The changes in the length frequency distribution of the flathead catch are thus seen to differ from expectation, but these differences are explicable on the above hypothesis. It would require no less than three "fallow" years to effect the appearance of a moderately large year-brood in the catchable stock, and five or six "fallow" years would be expected to provide a series of much larger year-broods. The rest actually afforded the flathead stock consisted of no more than two years of moderate fishing, followed by two years of virtually no fishing. In the year following, the fishing fleet was able to land the post-war maximum catch of flathead. The recovering flathead stock was hit very hard and was never able to make anything like a full recovery.

The aberrant year, 1947-48, in Figure 1 is now seen to be merely reflecting the inception of heavy catches in 1944-45; as a result of which the 1944-45 year-class (the 3-group in 1947-48) is deficient compared with those that went before it. By 1948-49 the proportion of the age-groups in Figure 1 has become readjusted—at a lower level.

There is significance for the above hypothesis in the apparent scarcity of the I-group of the flathead. In fisheries where the supply of recruits is limited only by natural fluctuations, the undersized fish are usually caught in great numbers by the industry in those years when they are abundant. Figure 2 shows an apparent poverty of the II-groups in classes 1944-45 and 1945-46, as well as of the III-groups. The details of the catch of flathead during this Division's experimental trawling using a covered codend were presented previously (Fairbridge 1951, Section I (*b*)). Even using this gear, it was found difficult to capture large samples of the I-group. After the first year, it was felt that we had a good idea of the general area of distribution of the I-group (within the 30 or 35 fathom contour); yet in the second year, even fewer I-group flathead were taken. The I-group taken in the first year were the 1946-47 year-group, and their greater abundance suggests a reflection of the more abundant spawning stock of that summer.

The fecundity of the species is not particularly relevant in assessing the validity of the hypothesis. Recruitment is governed by the mortality of the eggs and fry, as well as by the supply of eggs; and since we are ignorant of the mortality of the eggs, a knowledge of their initial numbers would not help. However, it is as well to add that, from general observations, the flathead appears to produce very much the same quantity of eggs as other small-egged species of about its size (e.g. the mullet). It does not appear to be deficient in this respect.

With more data it may be possible, in time to come, to correlate the rate of catch of the III-group with the fishing intensity of three years before, and establish whether there is an inverse ratio of high order. Of much greater value would be a continuance of experimental trawling using a covered codend, since by this means a more accurate estimate of recruitment can be obtained than is afforded by the marketed catch of the III-group. A perhaps secondary, but important, factor in the flathead's failure to recover is the limited size and life span of the species.

Hickling (1946) in his account of the recovery of the English hake fishery shows in his Table IV that the catch per trawler gross ton of "large and medium" hake increased about ten times in weight, while the catch of "small" hake increased by only about half. Most of the increase in the large and medium hake came within two years of the reduction of fishing. Thus the increase in rate of catch was largely a matter of permitting the existing individuals to grow to larger size.

It is strongly suggested in Part I of this study (Fairbridge 1951) that there is a relatively heavy natural mortality of the flathead, increasing from probably the IV-group onward. It is certain that few flathead can grow over 60 cm., or eight years old. Dakin (1939) says that Colefax measured a flathead of 67 cm. and several of 65 cm., and that these were considered exceptional by the fishermen in 1930. The present work confirms this size limit. If, then, there is indeed a heavy mortality from the IV-group onward, only a limited number of such fish can accumulate.

This is not to say that great benefit would not accrue from this source if fishing were relaxed.* The evidence of the early years suggests it would. In 1930, when the estimated flathead catch had been above 10,000,000 lb. for at least three years, Colefax (1934) was measuring random samples of flathead, the modes of the majority of which were over 40 cm. Today's mean mode (Fig. 3) is 34.5 cm. Many of Colefax's samples of large average size were from areas such as Green Cape, which had been fished from the very inception of trawling in New South Wales, though his samples from near Sydney showed modes at 24 and 32 cm. The data for the first half of 1938 (Fig. 3) shows that even in that year a much greater percentage of the catch was of IV-group fish. A four-year flathead weighs about 1 lb. as against 11 or 12 oz. for a three-year fish.

Nevertheless, we cannot expect large fish of 50 cm. and over ever to become dominant or even common in the flathead catch. It is in these size-groups that weight increases so rapidly. A five-year fish weighs about 1 lb. 10 oz.; the increase to this age-group is therefore nearly twice that of a three-year passing to four-year fish. In long-lived species, such as the cod and hake, the contribution to the weight of the catch by relatively few large specimens is very considerable.

Two other possible causes of the failure of the flathead to recover remain to be examined. One commonly hears the opinion expressed (among trawlermen) that it is the Danish seiners that have "ruined the fishery". It is difficult to be sure of the merits of this charge. There is no doubt that the Danish seiners catch a larger proportion of small flathead than the trawlers (Fig. 2). It is also true that they work closer inshore, and at times encroach on the shallow-water nursery grounds within 30 and 35 fathoms. This is the contour established by the experimental trawling outside which few of the very young flathead were taken. But to say from this that the very young flathead naturally occur only within this area may be unjustified; it may be that the larvae seek bottom in considerable numbers in water deeper than this, and the constant harrying by trawlers and Danish seiners may kill off all the young but those that happen to be in water shallower than is usually fished. If this alternative explanation has any truth in it, then the fact that the Danish seiners habitually work much more inshore than the trawlers is a serious argument in favour of trawlers against Danish seiners.

The history of the fishery between the two wars shows that the New South Wales trawlfishery could be fully exploited by the present fleet of trawlers alone (Fairbridge 1948) and that, from the point of view of supplying the public, there is no need for the Danish seiner fleet. Table 5 does seem to indicate the flathead catch falling with the inception of

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* There is a report that, in late February and early March 1945, there was a run of enormous flathead at both Eden and Ulladulla. The Danish seine fishermen had never seen anything like it. The fish were "about as long as the boxes" (i.e. 70 cm.). Market measuring was begun in the following May but none of these fish appeared in the results.

Danish seining; but the figures are not sufficiently reliable nor extensive to make the point.

Another suggested reason for the decline in the flathead stock has frequently been suggested to the author by trawlermen with experience of the Botany glut. The Botany ground is one of the closest to the trawlers' home port of Sydney. Until about 1926 there was every year a tremendous catch of flathead on this ground in September, October, and November (Colefax 1934). There is no doubt that this was a spawning concentration. Suddenly, so it is said, the Botany glut gave out and has never returned. Actually, the trawlers' logs from 1937 to 1942 do show that there was still some heavy fishing then on that ground at that time of year. As lately as 1948 there have been signs of a recurrence of the Botany glut; for ten days during September 1948 the bulk of the trawler fleet could be seen from the Cronulla laboratory fishing this ground, and it was reported that the ships were catching enormous quantities of undersized flathead (which, of course, were not marketed). An idea of the changed conditions can be gained from Table 6 of the catch on this ground by a number of vessels in the past.

TABLE 6

FLATHEAD CATCH FROM BOTANY GROUNDS

Year	Catch (million lb.)	Vessels Making the Catch
1919	2.3	7
1921	1.5	6
1922	1.5	7
1937	0.2	5
1938	0.2	14
1939	0.2	5

It thus appears that the catch on this ground in the early days of the fishery was more than 2,000,000 pounds, but just before the war in 1937 it had dropped to 250,000 pounds, and is today probably even less.

The situation is that though there is today seldom good fishing on the Botany ground, it is known to be a ground that occasionally provides very good fishing. Because it is just south of Sydney Heads, every trawler makes a shot there on her way to the southern grounds and perhaps on her way home. When a show of flathead appears, this is fished almost to extermination.

It is a great pity that no data exist of the catch from this ground during the war years and immediately after, when it had been rested. The good fishing obtained by the Danish seiners working from Sydney has been alluded to. It is probable that the Botany ground contributed materially to this.

It would seem a sound conservational measure to close this ground to fishing. A large stock of flathead there would contribute to the general catch not only directly by emigration, but by means of eggs and fry, which, it is suggested above, are a limiting factor in this fishery. The eggs and fry could be expected to be distributed by the strong New South Wales coastal currents. Moreover, it is only by some such experimental closure of a ground that it can be demonstrated whether or not the very young flathead are naturally confined to the shallow water, and that it is not a case merely of the shallow water protecting the young that happen to be there.

III. CONSERVATION

In the earlier paper dealing with the trawlfishery as a whole (Fairbridge 1948) it was urged that the trawling fleet (trawlers and Danish seiners) should be limited in size to the level during the middle 1930's, since the catch at this period seemed to be showing signs of recovery after evident overfishing in 1929. This fleet would be about 13 trawlers or the equivalent, in part, of Danish seiners. Action was urged to limit the fleet before it became even bigger than in 1946-47. The event has forestalled such action. Economic factors, but principally the shortage of fish, are now causing a reduction in numbers of the Danish seiners and are (perhaps) limiting the number of trawlers to 12. The total fishing effort, however, is still well above that of 1929.

Nothing in the present paper conflicts with the general conclusion arrived at previously that reduction of the fishing effort to about the equivalent of 13 trawlers is the first and prime requisite in rehabilitating this fishery.

If this were done, the flathead stock would be expected to recover gradually. The recovery would be expected to be slow at first, but of increasing speed as the stock of spawning adults increased and gave rise to larger recruit-broods. Considerable improvement in catches would be expected from the growth of many fish to larger size, though great improvements cannot be expected from this source. The calculated flathead catch shows that this species alone is capable of a sustained production of over 7,000,000 lb. annually, and probably a catch nearer 10,000,000 lb. is sustainable. Add to this the present catch of secondary species amounting to 11,000,000 lb., and the fishery would be producing 18-21,000,000 lb. Such a high figure is perhaps not altogether possible, since it may be that the supply of secondary fish has increased to fill the "niche" left by the flathead. However, no such absolute increase has been observed by the fishermen. This catch would be considerably more than the fishery has ever produced in the past, and it could be that a fleet larger than 13 trawlers would be necessary to land this catch. However, an initial reduction of the fleet to this size is a pre-requisite of such recovery.

Failing any reduction in the fleet from its present level, the condition of the fish stocks would not be expected to remain static but to worsen. The trawlers' catch of morwong and nannygai has risen very sharply, probably more than can be maintained. The rate of catch of the morwong has now declined for two years, and is little more than half its former level. Deteriorating stocks of these species would affect principally the trawlers. There are now no further secondary species to which to turn. As for the Danish seiners, the catch of flathead may or may not have stabilized itself round the present low level; an increase in the stock may begin to take place under the reduced fishing intensity by these vessels, but such an increase would not be widely felt before the trawlers began to join the Danish seiners. The excessive total fishing fleet would then again be felt and the flathead would make no permanent recovery.

As to the desirable or just proportion of trawlers to Danish seiners, the previous paper expressed no opinion, except to point out that the bulk of the fleet would always have to be trawlers, since only these vessels are able to fish the deeper waters off the coast and in Bass Strait. Figure 3 indicates that the trawlers catch a significantly greater proportion of large flathead than the Danish seiners. By regulating the mesh of the codend of the Danish seine, this gear could also no doubt be modified to spare the smaller fish. At present there is no law concerning the allowable mesh. A mesh of 2½ or 3 in. is the one most commonly used, and these in practice usually shrink ¼ in. on tanning and use. A little work has been done to compare the differences in catch between two such codends but not enough to reach any conclusion. The author is not of opinion that much good could be effected by increasing the mesh. Occasionally one hears of Danish seiners making large catches of undersized flathead and having to sweep them overboard, but the author's impression from a considerable amount of time spent fishing with these vessels is that such wastage is rare. There is a legal limit of 13 in. (33 cm.) on the flathead, which seems fair and reasonable in the light of its size at first spawning and short life-span. It is felt that, given a tolerable stock of flathead, as in the past, this regulation alone is enough to protect the small fish.

Figure 3 does, however, suggest an actual inability on the part of the Danish seiners to catch as many of the large, fast-moving flathead as the trawlers. The graphs for 1946-47, particularly, show this. This feature renders the trawler a much more desirable type of vessel for this fishery than the Danish seiner. The trawlers' tendency to catch fewer small fish and to work well away from the proven nursery grounds of the flathead are added advantages.

Closure of the Botany ground has already been discussed in this paper. It has been known in the past to be a most prolific breeding ground, and even of recent years, large numbers of I- and II-group flathead have on occasion been taken there. Total closure of this ground to trawling would be a highly valuable experimental measure. It is only in some such way that it would be possible to determine definitely whether or not the very young flathead occur naturally in water deeper than 35 fathoms. The ground would, of course, be sampled from time to time, using a trawl with covered codend, in order to determine the effects of the closure. The ground is immediately south of Sydney Heads and could easily be policed. An obvious alternative, or additional ground that might be closed to trawling, is that off Eden. It was in this area that the heaviest catches of O- and I-groups flathead were made during the experimental trawling. Closure of grounds, however, can only be an additional measure to general reduction of the fleet, and is in no way a substitute for this.

IV. Future Research

It is hoped to continue the routine sampling at the Sydney Fishmarket and the laboratory treatment of the data on a standard basis. This work provides a continuing and simple check on changes in the flathead stock, whether they arise from natural causes or from changes in the fishing intensity. The secondary species, morwong and nannygai, are also being sampled preparatory to making a study of their biology.

Little new work, however, can be attempted on the trawlfishery until the services of a vessel become available to carry out experimental trawling each year with a covered codend, and systematic tow-netting for the larvae. The experimental trawling, if carried on consistently from year to year, would be expected to give the only adequate check on recruitment into the fishery. It is of considerable theoretical as well as practical interest in the future to correlate recruitment with the stock of spawning adults, and hence prove or disprove the hypothesis that recruitment is dependent on the size of the spawning stock.

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STUDIES ON THE ECOLOGY OF THE NEW ZEALAND LONG-FINNED EEL, *ANGUILLA DIEFFENBACHII* GRAY

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Summary

Experimental trapping of eels, using carrion-baited traps, was carried out on a number of rivers of various types throughout New Zealand. Where possible, a mathematical analysis has been applied to the trapping results and an estimate of the efficiency obtained.

Total trappable population densities of between 30 and 1,358 lb./ac. were found. An attempt has been made to correlate type of river with the population density. The amount of cover present is apparently the limiting factor.

The baited trap takes very few eels of less than 24 in. long and is thus not a very efficient means of keeping a stream free from eels. The feeding habits of the eel are generalized and readily adaptable to most faunas. In most rivers trout occurred only infrequently in the stomach contents.

I. Introduction

The females of the long-finned eel, *Anguilla dieffenbachii* Gray (Griffin 1936), are commonly assumed to be harmful to trout fisheries, and in an attempt to improve the trout stocks much money and effort have been spent on their destruction—e.g. the Southland eel destruction campaign in 1937-38 (Cairns 1942*b*). Cairns (1942*a*) states, "The damage to the adult trout population from this predator must be enormous over a period of one year". There do not appear, however, to be sufficient data to justify such a sweeping statement. Owing to differences in habit and size, the male long-finned eel, and the short-finned eel, *Anguilla australis schmidtii* Phillipps (Griffin 1936), are not considered to be significant in this problem.

As yet no direct experiments have been done to measure the effect of the removal of eels from an area of water. In order to use this approach, considerable technical advances will have to be made in the measuring of trout population densities and survival rates.

The present series of investigations aims to provide the background knowledge necessary for any serious consideration of the effects on trout of competition for food, or of predation by eels. A general account of the accumulated information on eels is given by Bertin (1942), and a summary of available data relative to the eel-trout controversy is given by Hobbs (1948).

Information on the densities of eel populations in various trout waters is basic to the problem. The main aim in this investigation has been to obtain accurate estimates of the density and structure of eel populations, and to determine if possible the controlling factors. The data obtained

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would be of considerable use if commercial exploitation were being considered. The study of population densities has involved a study of the efficiencies of the methods of capture used, and this information would also be of practical value.

Additional data have been collected wherever possible. While the experiments were not designed for the study of feeding habits, some preliminary material has been collected. This will be especially useful for the design of further experiments.

The field work was done during the summers of 1947-48 and 1948-49. In 1947-48 (Section III) a number of rivers of various types were trapped in Southland. The following summer's work was done on a fairly typical river near Wellington, and later on a number of rivers of various types in the Waikato district.

II. Trapping Methods

The structural design of the traps used is shown in Plate 1. The framework is made from sheet reinforcing (7/32 in. steel rod), bent to form a cylinder 4 ft. long and 19 in. diameter. This framework is covered with galvanized wire netting, preferably of 1 in. diameter mesh. Smaller meshes are satisfactory but they make handling of the trap more difficult. Larger-size meshes are not suitable, as it was found that the eels could break their way out. The entrance cone is shaped from galvanized wire netting with an opening of 4 in. diameter left at the inner end. In the other end of the trap are fitted a basket for the bait and a semicircular trap door. The basic principle in the use of this type of trap is the provision of a line of scent leading the eel up through the entrance cone to the bait. Traps are thus best set in a moderate current of at least sufficient depth to cover the inlet and in such a way that the scent from the bait is carried down through the cone. It is also important to see that there is no tendency for the trap to vibrate or roll in the current, as this would frighten the eels. The eel is nocturnal in most waters and it was found that a baited trap would not attract them during daylight hours. In order to get the maximum effective scent from the bait the traps should thus be set as late as is practicable.

While most traps are similar to that illustrated, there are a number of modifications designed to make setting easier and to improve the efficiency. Two of the more common ones were tried. Firstly, a scrim or sacking cover was used around the trap in order to confine the scent. This should also provide shade and thus possibly diminish the tendency to escape after daylight. In practice the scrim makes the traps more difficult to handle and harder to set in moderate to fast currents. Secondly, a number of traps were fitted with strips of flax extending from the inner end of the entrance cone to the centre of the other end. This should prevent the escape of eels by making it more difficult for them to find the inlet once they are inside. As far as can be determined neither of these modifications significantly increased the efficiency of the traps.

Experimental trapping was done on selected areas of a number of streams. A constant number of traps was used, evenly spaced along the area, and trapping was continued for a number of nights. It was considered that analysis of the data so obtained would give information on trapping efficiency.

In order to derive a mathematical treatment for these results it has been found necessary to make a number of assumptions:

(i) That we are working on a closed population. This assumption requires that the original population shall not be affected by natural mortality or by movement into or out of the area. Owing to the short time involved in each experiment, a maximum of five days, natural mortality would have an insignificant effect. In the first areas examined movement was prevented by the use of wire-netting fences at both ends of the section being trapped. Further trapping was done without the use of barrier fences. The results obtained from each trap were examined for unexpectedly high catches and especially for any marked differences in the rate of catch. As far as could be determined only the last downstream trap was affected by the absence of barrier fences. It would thus appear that satisfactory results can be obtained by neglecting the catch in the last downstream trap.

(ii) That the unit of fishing effort remains constant. The number of traps employed and the spacing between them were kept constant for each experiment. It is necessary that the traps compete with each other, or there will be an unknown portion of the population that is not affected by the trapping. The individual traps will probably vary in efficiency from night to night according to how well they are set, but if there are sufficient traps in the unit this will not affect the results.

(iii) That the rate of catch remains constant. It has been assumed here that a fixed proportion of the surviving population is caught each night.

If these three assumptions hold, we can derive the following formula and then if the facts fit the formula it can be used to analyse the raw data. Let K = total population, and P = the proportion of eels caught in one night.

$$\text{Then first night's catch } C_1 = KP.$$

Therefore

$$\text{remaining population} = K - KP = K(1-P).$$

Then

$$\text{second night's catch} = C_2 = KP(1-P),$$
$$\text{third night's catch} = C_3 = KP(1-P)^2,$$
$$n\text{th night's catch} = C_n = KP(1-P)^{n-1}.$$

Therefore

$$\log C_n = \log K + \log P + (n-1) \log (1-P).$$

Thus if the three above assumptions hold, $\log C_n$ should be linearly related to n, the slope of the line being equal to $\log (1-P)$.

A similar approach to the problem has been made by De Lury (1947). While in the formula presented above the whole series of traps is a single unit of effort, De Lury considers each trap as a unit of effort, and is thus able to use material in which the number of traps in operation varies. To do this, however, one must also assume that the units of effort do not compete with each other, and that there is a random placing of the traps (or complete mixing of remaining population between each setting of the traps). This introduces other possible sources of error which are best avoided. Also the present investigation has been concerned with obtaining as complete a catch as possible, in a relatively short time, and for this reason as well as in order to avoid the possibility of dead spots, it was necessary to have competition between the traps.

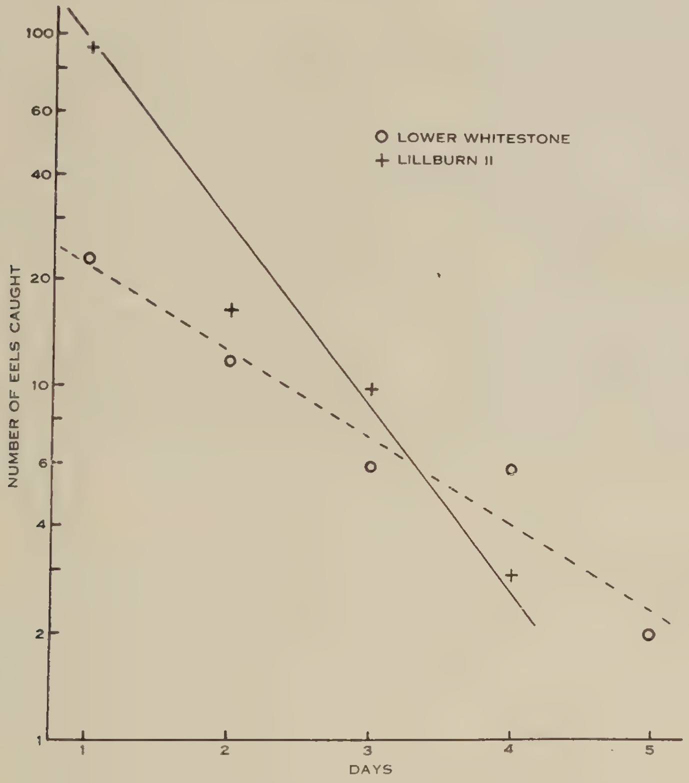

Fig. 1.—The number of eels caught each night follows approximately an exponential regression, and thus an estimate of the total trappable population can be obtained. The two sets of results shown illustrate different rates of catch (*P*).

A small experiment using traps baited with fresh rabbit was carried out. Five marked eels were replaced in the stream and a trap was set 100 yd. above the point. Four marked eels were replaced 200 yd. below the trap. The trap caught nine eels in six overnight sets, none of them marked. It was then moved down to the point where the first marked eels were replaced and there it caught seven eels, including two of the marked ones. This indicates that the maximum range of a trap is probably less than 100 yd. Further evidence comes from the area IV of the Wainui-o-mata River where a spacing of 154 yd. between traps was used.

After three sets at this spacing all the traps except the top one were moved upstream approximately 75 yd. It was found (Table 3) that at least 16 per cent. of the total population had not been taken at the original spacing. The maximum effective range, for ox liver bait, is thus less than 154 yd., and is probably between 100 and 120 yd.

The mathematical treatment was applied to seven of the trapping experiments with fair success. In all these cases, the type of bait used was the same (fresh rabbit) but the intensity of effort (spacing of traps) was varied from area to area. The figures when plotted (Fig. 1) do approximate to straight line relationships, but in all cases the samples involve too few eels to give any conclusive proof of the validity of the assumptions. It does, however, appear that the formula derived will give results sufficiently accurate for present purposes. As some of the factors to be correlated with these calculated population densities are capable of only very rough measurement there is little point in insisting on a high degree of accuracy.

TABLE 1

CATCHES OF EELS IN RABBIT-BAITED TRAPS

Location	Numbers Caught Each Day					P
	First	Second	Third	Fourth	Fifth	
Lillburn I	57	3	1	—	—	0.87
Flaxy	10	6	1	—	—	0.69
Lillburn II	93	17	11	3	—	0.67
Kakapo	82	23	10	5	—	0.60
Whitestone (lower)	23	12	6	6	2	0.43
Lillburn III	52	46	23	—	—	0.34
Whitestone I and III	33	24	7	—	—	Approx. 0.35

In the calculation of P it was found that the best results were obtained by treating the catches numerically instead of by weight. The figures, as shown in Table 1, were plotted logarithmically, and a straight line was fitted by the method of least squares. For all these areas the bait used was constant (fresh rabbit). The two variables that could account for various values of P are the spacing of the traps and the population density. The former can be expressed either on a linear basis as yd./trap or by area as traps/ac. (Table 2).

From this table it appears that P is related best to yd./trap. A plot of P against spacing of traps gave a good straight line relationship (Fig. 2). The Whitestone I and III point is the only one that does not fit this line closely. As it is thought that the range of a trap (baited with rabbit) is less than 100 yd., this point cannot be expected to fit the straight line relationship. This graph also enables us to calculate, for various trap spacings, the amount of effort (trap days/100 yd.) required to remove 90 per cent. of the trappable population. The formula $C_n = KP(1-P)^{n-1}$ can be expressed as, percentage caught $= 1-(1-P)^n \times 100$. Then for $n = 1, 2, 3, 4$, and 5, the values of P required for 90 per cent. removal

TABLE 2

VARIATION OF RATE OF CATCH (P)

Location	P	Spacing of Traps (yd.)	Traps/Ac.	Population Density (lb./ac.)
Lillburn I	0.87	13.2	16.5	135
Flaxy III	0.69	44	5.0	106
Lillburn II	0.67	41.8	5.1	90
Kakapo	0.60	55	17.7	1358
Whitestone (lower)	0.43	96.8	2.3	76
Lillburn III	0.34	94.6	2.3	105
Whitestone I and III	0.35	132	1.7	30

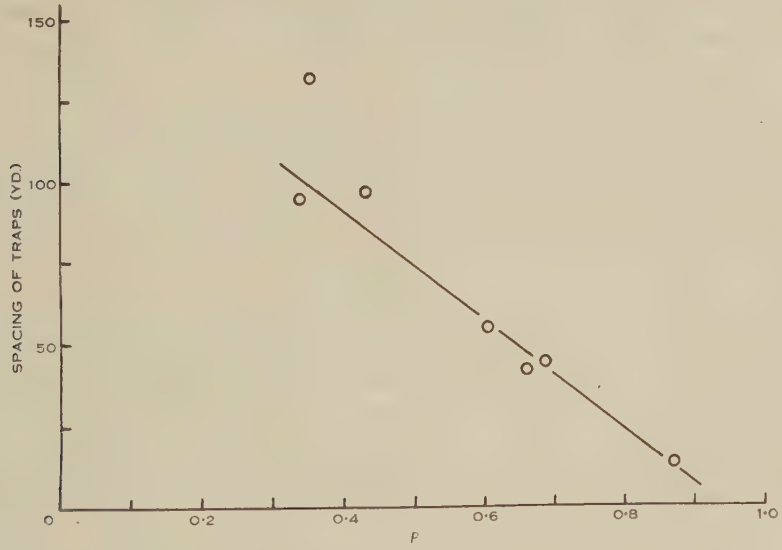

Fig. 2.—Over the working range of the traps there is a good linear relationship between the spacing of the traps and the rate of catch (P).

of the trappable population can be calculated. The corresponding spacing of the traps can be obtained using Figure 2. We thus have the data to plot effort (trap days/100 yd.) against the spacing of the traps (Fig. 3). From this it can be seen that the minimum effort is required when three overnight sets are used with a spacing of about 67 yd. between traps. The main practical point arising is the inefficiency of a single overnight set at the close spacing required for 90 per cent. removal. Owing to the limited range of the traps the graph has not been extended beyond 100 yd.

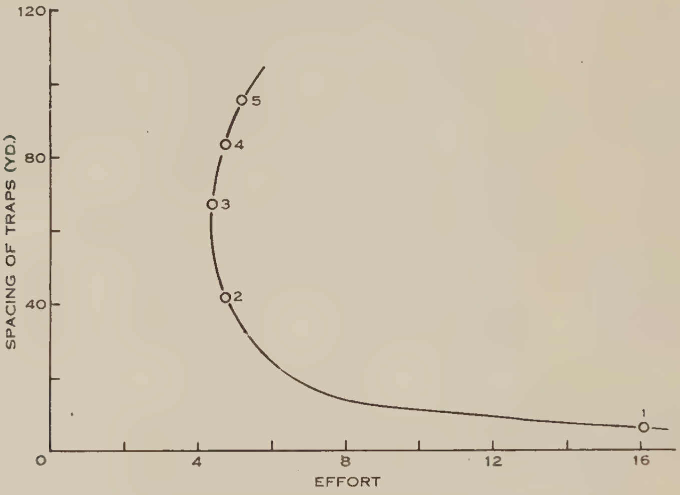

Fig. 3.—Amount of effort required to remove 90 per cent. of the trappable population when from one to five settings of the traps are used.

TABLE 3

CATCHES OF EELS IN TRAPS BAITED WITH OX LIVER AND SPLEEN

Wainui-o-mata R.	Spacing of Traps (yd.)	Numbers Caught Each Day			
		First	Second	Third	Fourth
Area I	44	22	0	2	—
Area II	58.7	25	0	Interrupted by fresh	
Area III	77	7	11	1	—
Area IV	154	43	1	2	9*

* All traps (except top one) shifted up half a space for this set.

On the other hand a maximum catch, irrespective of the degree of exploitation of the population, is obtained when a single overnight set is used with a sufficiently wide spacing to make competition between the traps insignificant.

Liver has also been used as bait but the foregoing treatment could not be applied because the results (Table 3) would not fit an exponential regression. From a general examination of the figures it would appear that the efficiency is somewhat higher than for rabbit and that the range is limited to about 100 yd., as with rabbit.

A number of eels were caught in the Wainui-o-mata River by the use of hand nets and gaffs at night. For this method a selected area of the river was examined at night (between 9 and 12 p.m.) using electric torches. The two operators attempted to catch all eels seen, either by gaffing them out or by manoeuvring the eel into a hand net. This work was carried out for a number of successive nights on each selected area. The results so obtained, although irregular, showed a tendency for the catch to decrease with time (Table 4). The significance of this decrease can best be tested by applying the exponential regression hypothesis. The exponential regression line was fitted by the method of least squares (e.g. see Fig. 1). The agreement shown between the three values of P is much better than would be expected, taking into consideration the probable variability of intensity of effort with this method and also the small number of eels involved.

TABLE 4

CATCHES OF EELS WITH HAND NETS AND GAFFS

Wainui-o-mata River	Gaffed Eels—Numbers Caught Each Night				P
	First	Second	Third	Fourth	
Area I	11	8	4	6	0.22
Area II	13	10	—*	—*	0.23
Area III	8	5	5	—*	0.21

* Nights not fished.

The results obtained throughout all this work were remarkably constant. Only twice were unusually low catches obtained, in both cases during a fresh. There is thus no support for the belief that weather conditions affect the efficiency of trapping.

All the relevant data for the various trapping experiments are set out in Table 5. Where possible the rate of catch has been calculated using the formula already presented. Then total percentage of the trappable population caught $= 1 - (1 - P)^n \times 100$. Where values for P were available, the total percentage caught has been calculated (Table 5). Using this percentage, the total possible yield was calculated from the catch (lb./ac.). The Wainui-o-mata series, where a different bait was used (ox spleen and liver), did not give trapping curves that could be treated mathematically. Also, in the Waikato series, considerable difficulty was experienced owing to faulty traps. For these cases an alternative criterion was necessary and it is considered that, if the final night's catch

TABLE 5

RESULTS OF TRAPPING EXPERIMENTS

River	Total No. Caught	Amount Caught on Last Night (%)	$1-(1-P)^n \times 100$		Effort (trap days /100 yd.)	Spacing (yd.)	Total Area (ac.)	Total Catch (lb.)	Catch (lb./ac.)	Total Possible Yield (lb./ac.)	
			P	(%)							
Kakapo	120	4.2	0.60	97.5	7.3	55	0.34	450.2	1324	1358	
Flaxy (upper) I	19	5.3	—	—	4.5	44	0.055	71.5	1312		1120
Flaxy (upper) II	22	9.1	—	—	2.3	88	0.073	67.7	927		
Kaniwhanawhana	71	9.9	—	—	7.6	66	0.38	195.9	516		
Waipa	206	3.9	—	—	11.4	44	2.0	549	275		
Flaxy (lower)	17	5.9	0.69	96.9	6.8	44	0.60	61.9	103	106	
Lillburn I	61	1.6	0.87	99.8	22.7	13	1.45	195.6	135	135	103
Lillburn II	124	2.2	0.66	98.6	9.3	42	4.5	400.0	89	90	
Lillburn III	122	17.4	0.34	70.6	3.1	95	5.2	386.8	74	105	
Whitestone (lower)	57	3.5	0.43	93.9	6.2	97	2.6	189.1	72	76	
Ngakoahia I	14	14.3	0.8 approx.	95	1.5	132	1.2	56.7	40	55	
Ngakoahia II	16	37.5	0.4	64	1.7	176	1.6	55.5		(Estimated)	
Wainui-o-mata I	24	8.3	—	—	6.8	44	1.3	62.7	48		39
Wainui-o-mata II	25	nil	—	—	3.4	59	2.1	68.5	32		
Wainui-o-mata III	19	5.3	—	—	3.9	77	2.8	72.0	26		
Wainui-o-mata IV	56	—	—	—	2.6	154	4.2	202.9	41		
Whitestone (upper)	64	10.9	0.35	72½ for 100*	2.3	132	10.8	174.1	16	30 (Estimated)	

is less than 10 per cent. of the total, then for all practical purposes the yield is complete. For the Ngakoahia and Upper Whitestone, rough estimations have been made using the trapping rate and allowing for the fact that the traps were working beyond their effective range.

III. TRAPPING YIELDS

It will be shown that the results to be discussed refer only to a proportion of the total population (see length frequency curves Fig. 4*B*). Although the smaller eels are not taken into account, the results obtained are those of importance where commercial exploitation or predation on trout is being considered. A little information has been obtained on the smaller size-groups, but as yet there is no really efficient method for their capture.

In Southland, trapping was carried out on tributaries of the Waiau River. The first area was the Lillburn River, which is within 20 miles of the sea. In the second area, the Whitestone River and tributaries (90 miles from the sea), a range of different types of waters was examined. It did not appear that the distance from the sea affected the results (Table 6). Further trapping was done in the Wellington and Waikato districts on rivers similar to those examined in Southland. The results from these areas did not indicate any difference due to variation in latitude. It was apparent, however, that the yield could be correlated with the type of river. In general the low yields were obtained from the open shingle bed rivers, and the high yields from stable rivers.

As the eel is nocturnal in almost all streams, it is possible that a factor limiting the density of populations is the number of suitable niches where the light is sufficiently subdued for them during the day. Anything that provides this type of niche will be referred to under the general classification of cover. In Table 6 the rivers have been briefly described from this point of view. While this is only a very general treatment it is obvious that decreasing cover can be correlated with decreasing yield, even if the mode of operation is not as suggested.

The rivers in Table 6 can be divided into three groups:

(i) High yield—250 lb./ac. and above. These are stable streams with good cover in the form of heavy weed growth, overhung banks, or deep, turbid water.

(ii) Low yields—60 lb./ac. and less. Moderately stable to unstable streams, open shingle beds, and little cover other than a few pools.

(iii) Moderate yields—100 lb./ac. Two of this group are streams of moderate stability, with some good cover. The third is a stable stream, where the value of the weed cover is probably limited by the depth.

If cover is the limiting factor, then the yield of any section of a stream should be determined by the amount of cover in that section. For three of the rivers trapped, the Lillburn, Whitestone (lower), and the

TABLE 6

TRAPPING RESULTS FOR EACH AREA

River	District	Distance from Sea (miles)	Fauna Density	Type of Bed†	Weed‡	Pool Depth	Other Cover	Water	Total Yield (lb./ac.)
Kakapo Stream	Southland	70	489*	Stable	Heavy	Uniform 4-5 ft.	Banks generally overhanging	Clear	1358
Flaxy Ck. (upper)	Southland	70	—	Stable	Light	Uniform 2 ft.	Banks overgrown with flax	Clear	1120
Kaniwhanawhana R.	Waikato	90	—	Stable	Moderate	3-4 ft., with a few deeper holes	Some fallen timber	Clear	516
Waipa R.	Waikato	90	—	Stable	Light	Uniform 10-15 ft. (bottom not visible)	Little fallen timber	Turbid	275
Flaxy Ck. (lower)	Southland	70	—	Stable	Moderate	Uniform 2 ft.	Nil	Clear	106
Lillburn R.	Southland	20	369	Moderately stable	Very light	50% pool 4-8 ft. (Bottom of pools not visible)	Little fallen timber and some overhanging banks	Slightly turbid	103
Whitestone R. (lower)	Southland	70	653	Moderately stable	Nil	25% pool 4 ft.	Some fallen sod	Clear	76
Ngakoahia R.	Waikato	90	454	Moderately stable	Nil	14% pool 2-3 ft.	Little overhanging banks	Clear	Approx. 55
Wainui-o-mata R.	Wellington	Lower 10	540	Moderately stable	Very light	38% pool 5-6 ft.	Nil	Clear	39
Whitestone R. (upper)	Southland	70	736	Unstable	Nil	Uniform 1-2 ft.	Nil	Clear	Approx. 30

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* Animals per sq. ft.

† Stable: stream confined by stable banks — little or no erosion; Moderately Stable: some shingle beaches, main channel fairly permanent and well defined; Unstable: open shingle bed, shifting channel.

‡ Heavy: complete coverage of bed; Moderate: isolated patches of bed visible; Light: numerous patches of weed; Very Light: occasional patches of weed.

TABLE 7

TRAPPING RESULTS ACCORDING TO TYPE OF COVER

Type of Water		Lillburn R.			Whitestone R. (lower)			Wainui-o-mata R.		
		No.	Range (lb./ac.)	Mean (lb./ac.)	No.	Range (lb./ac.)	Mean (lb./ac.)	No.	Range (lb./ac.)	Mean (lb./ac.)
Pools, deep (over 6 ft.)		8	137-377	242	1	—	110	2	90-125	107
Pools, shallow		10	75-155	118	Nil	—	—	6	49-72	58
Flats and stickles over 1 ft. deep	With deep, overhanging banks	1	—	185	Nil	—	—	Nil	—	—
Flats and stickles over 1 ft. deep	With fallen timber	2	90-173	131	Nil	—	—	Nil	—	—
Flats and stickles over 1 ft. deep	With fallen sod banks	Nil	—	—	2	76-120	98	Nil	—	—
Flats and stickles over 1 ft. deep	With moderate overhanging banks	7	40-114	82	2	72-94	83	2	76-107	92
Flats and stickles over 1 ft. deep	Open, with no apparent cover	14	10-45	29	Nil	—	—	5	18-45	31
Flats and stickles less than 1 ft. deep	Open with no apparent cover	Nil	—	—	2	20-24	22	6	4-14	10

Wainui-o-mata, it has been possible to describe the cover present in the section of the river fished by each trap. The yield (lb./ac.) was then worked out for each section and the results are shown in Table 7. The validity of the cover hypothesis is supported by the agreement, from river to river, for each type of cover. With the Lillburn pools it is thought that their cover value is enhanced by the slight turbidity of the water.

The data from the Ngakoahia and the Whitestone (upper) have not been used as there is some doubt as to what proportion of the total trappable population was caught. The Waipa River, in the area trapped, can be classified as a uniform deep pool with turbid water and as such agrees with the results presented in Table 7. In the remaining streams there are varying combinations of a number of cover factors and it has not proved possible to analyse for each separately.

IV. Population Constitution

As most of the information on population densities has been obtained by the use of baited traps, it is important to consider just what is meant by the trappable population. The length frequency curve for all eels caught by the use of baited traps in the Wainui-o-mata River is shown in Figure 4*B*. Compare this curve with Figure 4*A*, which is the length frequency curve of all the eels taken by the use of hand nets and gaffs in the same area. The eels actually sampled were those that were moving in the stream at night and no attempt was made to chase eels out of cover. It can be seen that very few of the smaller eels less than 12 in. long were taken by this method. The smallest eels are not available as they live in mud, or hidden under stones, etc. (cryptozoic). The rapid change in habit to a phanerozoic way of life, between 12 and 14 in. long, is shown in Figure 4*A*. MacFarlane (1936) also concluded, from a study of the parasites of eels, that there is a change in feeding habit at a length of 35-40 cm. Infestation with the trematodes *Opechona* and *Telogaster* occurs through eating either trout, bullies (*Gobiomorphus* spp.), or *Galaxias* spp. He found no infestation in eels of less than 40 cm. and, for eels above 40 cm., increasing infestation with size.

The failure of baited traps to catch the smaller eels that are present in the streams (Fig. 4*A*) is apparently due to the method of trapping used (i.e. the use of carrion bait). The results obtained from a number of traps covered with very fine mesh netting showed that the smaller eels do not enter the baited trap. There is thus a second change of habit, the appearance of carnivorous tendencies, which is apparently fully developed when the eel is 30 in. long. It will also be shown later that trout-eating tendencies first become significant when the eel is about 28 in. long.

It has been assumed that the baited trap is capable of catching all eels of 30 in. and above. Of the eels less than 30 in. long, only a proportion are taken, and at present there is not sufficient information to make an estimate of the total population density. The transition from non-trappable to completely trappable is very rapid, especially when considered in terms of years of growth. Figure 4*E* shows the age in years (Cairns 1941) marked against the lengths.

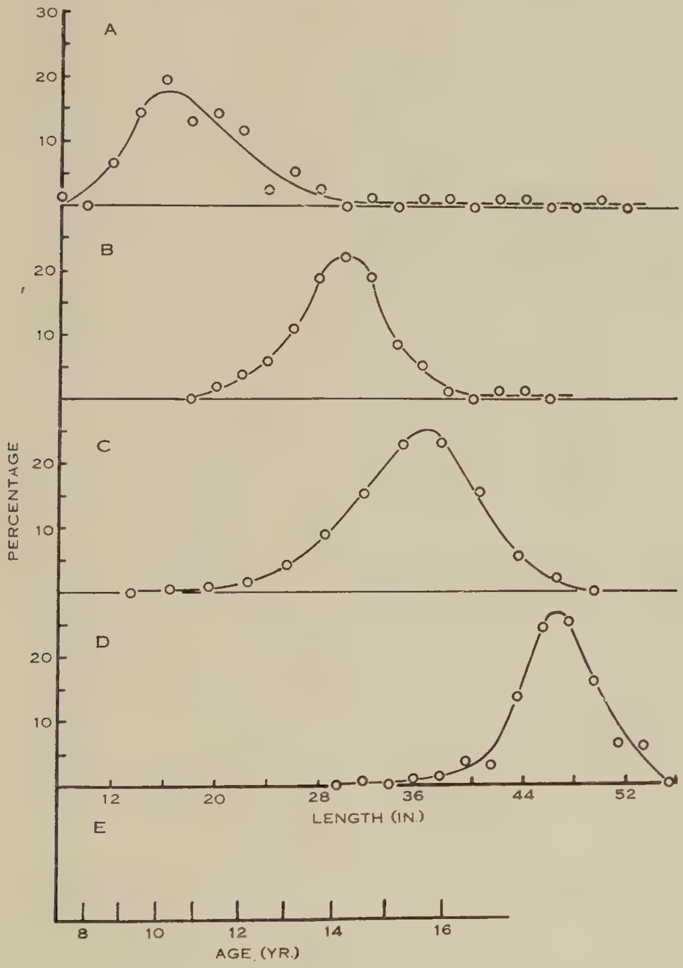


Fig. 4 (*A-D*).—Length frequency curves for:
A. Wainui-o-mata River eels taken with a hand net and gaff,
B. Wainui-o-mata River eels taken in a baited trap,
C. Lake Wanaka eels taken in a baited trap,
D. Migrant eels from Lake Ellesmere.
E. Age in years (Cairns 1941).

It was not expected that so few of the larger eels would be taken by the hand net and gaff method. It is probable, however, that in the river worked most of the cover for the larger eels is in the form of deep pools and these are not accessible to this method of capture.

The length frequency curve for the Wainui-o-mata River trapped eels is generally typical of all the areas trapped. No significant variations

TABLE 8

PERCENTAGE COMPOSITION OF CATCH

Location	15-18 in.	18-21 in.	21-24 in.	24-27 in.	27-30 in.	30-33 in.	33-36 in.	36-39 in.	39-42 in.	42-45 in.	45-48 in.	48-51 in.	51-54 in.	54-57 in.	No. in Sample
Wainui-o-mata (baited trap)	—	2.0	5.8	14.9	28.6	31.1	12.3	2.6	0.7	2.0	—	—	—	—	154
Lillburn R. (baited trap)	—	1.3	7.5	23.3	25.6	16.7	12.8	7.2	3.9	1.0	0.7	—	—	—	305
Kakapo R. (baited trap)	—	—	1.5	9.1	19.7	30.3	25.0	8.3	4.5	1.5	—	—	—	—	132
Whitestone R. (baited trap)	—	—	11.3	25.8	24.7	18.5	12.4	4.1	3.1	—	—	—	—	—	97
Waipa R. (baited trap)	—	3.1	12.5	31.4	25.1	18.4	5.4	2.2	0.9	0.4	0.4	—	—	—	223
L. Wanaka (baited trap)	0.4	0.8	1.5	4.2	8.9	15.2	22.8	23.1	15.4	5.5	2.1	—	—	—	618
L. Ellesmere (non-migrants — Hobbs)	—	—	—	—	—	7.1	7.1	25.0	17.9	21.4	17.9	3.6	—	—	28
L. Ellesmere (long-fin female migrants)	—	—	—	—	—	0.6	1.1	3.4	4.0	24.9	38.4	16.4	11.3	—	177

were found in other waters (Table 8). Figures available from other sources, Cairns (1941), Southland Acclimatization Society (unpublished data, Waihopai and Waikiwi Rivers trapped 1947-48), and from the Department of Internal Affairs (unpublished data, Southern Lakes eel trapping campaign 1948-49), all agree remarkably well, except with eels caught in Lake Wanaka. Here the average size of eels caught is somewhat larger (Fig. 4*C*). At present no explanation of this one divergence can be offered as nothing is known of the factors influencing the age at which eels migrate and little is known of growth rates.

The only detailed study of the sizes of migrant eels is that done by Hobbs (1947) on Lake Ellesmere. The average length of the female *Anguilla dieffenbachii* migrants was 47 in., which does not link up at all well with the sizes of river eels caught (Fig. 4*D*). Cairns (1941), on the other hand, from general observations states that the long-finned eel is usually mature at about 90 cm. (35.4 in.).

It is not likely that the larger eels have a very high mortality rate as they have few natural enemies. However, from Figure 4*B* the survival rate for 15-16 years (33-37.4 in.) is 23 per cent. If this low figure is due to the migration of maturing eels, then the average size of the migrants would be of the order of 36 in. (7 lb.) which is considerably smaller than those found in Lake Ellesmere, and similar to the size suggested by Cairns (1941). If, on the other hand, the river migrants are comparable in size to the Ellesmere migrants then there will be relatively few of them. It is possible that Lake Ellesmere is a special case. D. F. Hobbs (personal communication), when sampling the non-migrant population, took in the Taumutu area a sample, the average length of which was intermediate between that of the river eels and the migrants. Also in Lake Wanaka the average length of the eels trapped was greater.

An attempt has been made to determine the rate of replacement of trappable eels following complete trapping. To do this it is necessary to assume that: (i) All eels of 30 in. and longer are completely trappable, (ii) The removal of the trappable population does not affect the mortality rate of the unexploited stock or the development of characteristics that make that stock trappable. In practice it is probable that the mortality rate would be decreased and thus the replacement rate calculated on the above assumptions is a minimum.

Nothing is at present known of the mortality rate of eels of less than 30 in. but it is possible automatically to compensate for this by assuming a zero mortality rate up to 30 in. (the effect of this assumption can be seen in Table 9). The length frequency curve for trappable eels represents approximately five years growth (Fig. 4*B*). In order to simplify the calculation the fish in each year-class are taken as being identical in length. Also the 14-year group has been moved to 30 in. in order to coincide with the peak of the length frequency curve.

In Table 9, line 2, is shown the percentage of each year-class that would be taken by baited traps, if there were no mortality up to 30 in. (14 years). Line 3 gives the survival rate from 14-15 years and from 15-16 years. The latter figure differs slightly from the one previously quoted owing to the different placing of the age-groups. A catch of 100 eels would be distributed in the age-groups as shown in line 4. Then the population remaining (assuming zero mortality rate) is shown (line 5). If these figures are moved across one year (line 6) and the trapping percentages of line 2 applied, we obtain the theoretical trappable population for the first year following complete trapping. Similarly the figures are moved across for the second, third, and fourth years. When moving a figure from the 14-15 year and from the 15-16 year columns, the survival percentages shown in line 3 have been applied.

TABLE 9

RATE OF REPLACEMENT*

							Total Number	Total Weight (lb.)	Weight (%)
1 Age (yr.)	11	12	13	14	15	16			
2 Percentage of age-group trappable	5.8	20.4	50.2	100	100	100			
3 Survival rate (%)					39	18			
4 Trappable population	2.6	9.2	22.6	45.0	17.5	3.1	100	304	
5 Numbers remaining	42.4	35.8	22.4	0	0	0			
6 + 1 year	45.0	42.4	35.8	22.4	0	0			
7 Number trappable first year	2.6	8.6	18	22.4	0	0	52	119	39
8 + 2 years	45.0	45.0	42.4	35.8	8.7	0			
9 Number trappable second year	2.6	9.2	21.3	35.8	8.7	0	78	209	69
10 + 3 years	45.0	45.0	45.0	42.4	14.0	1.6			
11 Number trappable third year	2.6	9.2	22.6	42.4	14.0	1.6	92	268	88
12 + 4 years	45.0	45.0	45.0	45.0	16.5	2.5			
13 Number trappable fourth year	2.6	9.2	22.6	45.0	16.5	2.5	98	295	97

* This table is based on Figure *4B*.

The numbers of eels in Table 9 can be converted to weights using Figure 8 and the corresponding percentage rate of replacement calculated. This is slightly slower than the numerical replacement. It must be remembered that these figures are at best a very rough estimate, but it does appear probable that a good crop of eels could be taken every third year.

A cropping of this nature, where all the eels are removed before they reach maturity, can only continue when the population being exploited is small in relation to the whole population. The migration and spawning habits of the eel, with the consequent random distribution of the progeny, make the whole of the species a single population. Thus an eel fishery could exploit a limited area at least to the extent shown in Table 9 and with the probability of a continuity of supply.

V. Length-Weight Relationship

The length-weight relationship has been examined for four samples, each from a definite limited area and each containing the majority of the trappable eels in that area. The plot of weights against lengths gave a curve that indicated the possibilities of a logarithmic relationship. This was tried and in all cases the results gave the appearance of being a straight line over the complete range (12-50 in.). If this is the case, then the following formula can be applied:

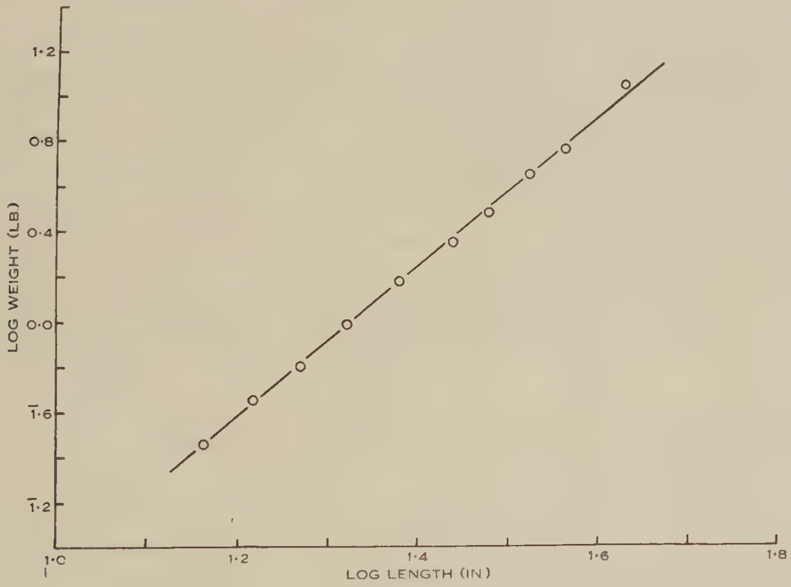


Fig. 5.—The length-weight relationship for all eels taken from the Wainui-o-mata River. The points shown are the grouped log means for the 242 values obtained. The regression line shown was calculated from the means by the method of least squares, and is

$$\log \text{Wt.} = 3.305 \log L - 4.387.$$

The standard deviation from regression, calculated from all the individual points = 0.054.

$$\log \text{Wt.} = n \log L + k$$

or

$$\text{Wt.} = KL^{(n)} \text{ (where } K = 10^{-k}\text{)}.$$

This formula is one that has been used extensively in fisheries work. The value of n has usually been assumed to be 3; i.e. the weight is proportional to the cube of the length. The factor K, known as the condition factor, provides a means of comparing variations of weight with length when fish of differing lengths are being considered. For the samples of eels examined, however, it was found that the value of n was slightly greater than 3.

A number of authors have examined the length-weight relationship critically and found n to vary from 3. Marr (1943) gives values of less than 3 for two species of Columbia River salmon. A full discussion of the significance of variations in n and a bibliography are given by Martin (1949).

The four regression lines obtained for the samples shown in Table 10 were compared and the differences found were small when compared with the spread of the points for each line. This is of interest, especially as the four samples compared represent wide differences in geographic location and type of river from which the eels were taken. There is thus no evidence that environmental conditions affect the growth pattern. This may be due to the slow growth rate of eels.

TABLE 10

LENGTH-WEIGHT RELATIONSHIP FOR CERTAIN AREAS

River	No. in Sample	n
Kakapo	128	3.22
Lillburn	313	3.15
Wainui-o-mata	242	3.31
Waipa	223	3.13

Shorland and Russell (1948) expressed the length-weight relationship for long-finned female eels in a linear form involving the use of two formulae:

$$52\text{-}89 \text{ cm.} \quad W = 38.45\ (L - 43.51 \text{ cm.})$$

$$\text{Over } 89 \text{ cm.} \quad W = 187.7\ (L - 91 \text{ cm.}).$$

The inflection was considered to be due to the development of the ovary.

The author has not, however, found evidence of an inflection point in any of larger samples examined. Also, the data presented by Shorland and Russell can be expressed by a formula of the type:

$$W = KL^{(n)},$$

and there is no reason why this generally accepted single formula should not apply.

VI. Feeding Habits

(*a*) *Other Than Fish*

The stomach only was removed and preserved in formalin as soon as possible after the fish was caught. Three methods of storage were used:

(i) The stomach and a numbered metal tag were placed in a small bag, and thus a number of stomachs could be stored in one jar.

(ii) The numbered tag was placed inside the stomach and the openings were tied. As in the first method several stomachs could be stored in one jar.

(iii) The stomach contents were emptied into a numbered 4 × 1 in. specimen tube (or larger where necessary), and mixed with 4 per cent. formalin.

While method (iii) was more difficult in the field, the stomach contents were easier to analyse. In methods (i) and (ii) shrinkage of the stomach often compressed the contents into a tangled mass which was frequently set in precipitated mucus.

The main analysis of the data was done by the numerical method. This method is the easiest to use where correlations between the feeding habit and the bottom fauna are being considered. Also it is the only method suitable for partially digested material. The dominance method was used for preliminary analysis to show the general trends and thus plan more detailed analysis.

The numerical method does not, however, give all the information necessary, and wherever there was no apparent digestion of the stomach contents each type of animal was weighed as well as counted. The animals were placed in weighed, numbered tubes, dried for 72 hours in an oven at 60°C., and then weighed. This technique avoids the practical difficulties of accurate wet weighing. Although the weight method is valuable in that it shows the relative value of different animals where there is a disparity of size (not necessarily shown by number method), it can be misleading unless allowance is made for heavy, indigestible parts.

In the following analyses all the dry weights have been converted to wet weight of animal only (excluding the weight of the case). This wet weight is more representative of the food value of the animals and also comparable to the type of food used in feeding experiments. The conversion factors used were experimentally determined by K. R. Allen (personal communication) and they are given in Table 11.

Whenever possible quantitative faunistic samples were taken. The animals were collected with a square foot shovel, sorted, counted, and weighed, using techniques similar to those described by Allen (1940). In most cases four samples were taken in each area, two from a stickle and two from a flat.

The majority of the stomachs examined were from eels caught in a baited trap. A sample of 64 stomachs from specimens taken at night with a hand net and gaff was also examined. Neither method is satisfactory for a fully quantitative study. While it is probable that the attraction of the bait would disturb the normal feeding pattern, material obtained using baited traps does, however, appear to be satisfactory for the determination of the relative numbers of the various animals eaten. With the hand net and gaff method the eels were probably taken before they had finished feeding. The percentages of eels with food in the stomach are given in Table 12.

TABLE 11

CONVERSION FACTORS: DRY WEIGHT TO WET WEIGHT (ANIMAL ONLY)

Eel Food	Conversion Factor
Trichoptera (sand-cased)	0.5
Mollusca	2
All caseless insects	4

TABLE 12

EELS WITH FOOD IN STOMACH

River	Method	Number Examined	Number With Food (%)
Waipa	Baited trap	223	35
Kaniwhanawhana	Baited trap	98	33
Wainui-o-mata	Baited trap	169	37
Wainui-o-mata	Hand net and gaff	77	83

It has been already shown that the gaffed eels are smaller than those taken in a baited trap. When the figures are extracted for the various size-groups and plotted (Fig. 6), there is a distinct tendency for the number of empty stomachs to increase with the size of the eel. It must be remembered, however, that this tendency is not necessarily the true feeding pattern and may be due to the method of capture used. If the time of commencing to feed varies with size, then both methods would give this type of result. Also for the trapped eels it is quite possible that the attraction of carrion bait is stronger for the larger eels and so they have less opportunity to feed before capture. The small numbers of larger eels seen feeding at night (Fig. 4*A*) suggests less frequent feeding but again this could be due to the method of capture used.

The average number of animals per stomach varies with the size of fish but not to the extent that would be expected if the larger fish were feeding less frequently (Table 13).

During the sorting of the stomach contents it was noticed that a number contained almost entirely one type of animal. It would thus appear that some of the eels were not feeding at random on the available fauna, taking Allen's (1941*a*) definition of these terms. Hess and Swartz (1940) recognized both preferences and availability but made no attempt to separate the two effects for their "forage ratio".

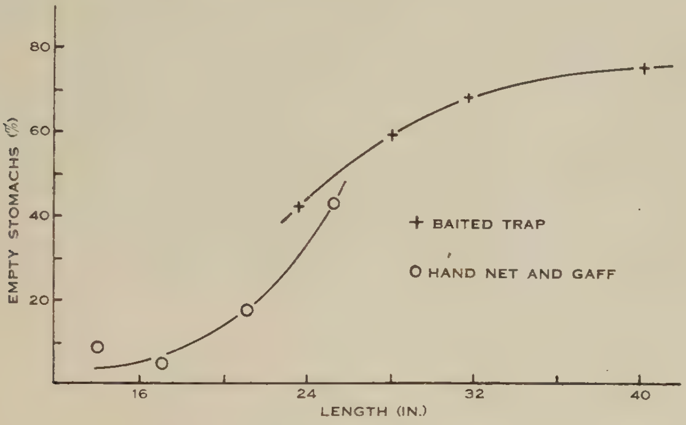


Fig. 6.—For both the gaffed and the trapped eels the number of empty stomachs encountered increases with the size of the eel. It is probable, however, that this is an effect due to the methods of capture used.

TABLE 13

AVERAGE NUMBERS OF ANIMALS PER STOMACH FOR WAINUI-O-MATA R. EELS

Eel Length (in.)	Eel Mean Weight (kg.)	No. of Animals per Stomach	No. of Animals per kg. of Fish
Up to 20	0.177	41	232
20-28	0.626	105	168
Over 28	1.59	548	345

Type of Catch	Eel Mean Weight (kg.)	Mean Weight of Food (g.)	Percentage of Body Weight
Gaffed eels	0.28	0.435	0.15
Trapped eels	1.31	1.51	0.12

The selection effect has been fully discussed by Allen (1941*b*) and use has been made of the methods of analysis developed. In Figure 7 the percentage of the dominant animal (irrespective of species) has been plotted against the number of animals in the stomach. The first portion of the curve, representing up to 10 animals per stomach, follows the general trend for random feeding. The upward trend would not occur if the eels were feeding at random on the available fauna. In order to demonstrate the significance of this effect a division has been made at 30. It has been assumed that those with less than 30 animals in the stomach contents have been random feeding, or exercising only a little selection, and that those with more than 30 animals in the stomach contents have, to some extent, been selecting one particular animal.

In the tabulation of the stomach contents three factors have been taken into consideration: selection, size of fish, and composition of the bottom fauna. Where the data are split up in this way, a number of the groups represent only a few stomachs and it is thus possible to indicate only general trends. For this reason only two size-groups have been used, and the division has been made at 24 in., as it is at this size that carnivorous tendencies become significant.

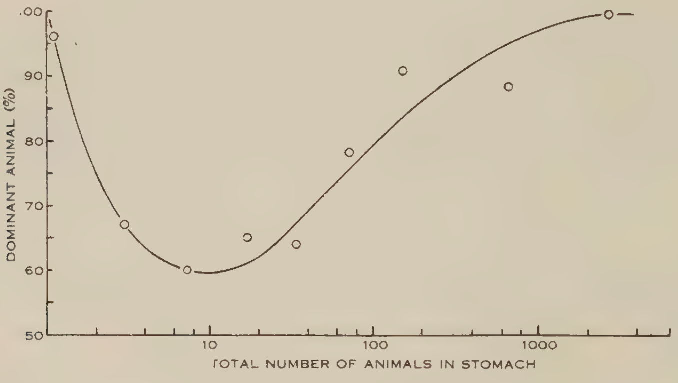


Fig. 7.—The relation between the percentage of the dominant animal and the total number of animals in the stomach contents.

The effects of the above factors are best demonstrated by the more important groups (Table 14). In all cases, whether selection is operating or not, the percentage of Ephemeroptera taken decreases with increasing size. Also in all cases the percentage of Trichoptera increases with the size of the fish.

The major faunistic difference between area I and areas III and IV is the occurrence of a very much lower percentage of Ephemeroptera and a higher percentage of Trichoptera in the latter. The decreased Ephemeroptera fauna results in a lower percentage of Ephemeroptera in the stomach contents, as can be seen by the comparison of corresponding figures in Table 14. While in the random groups (up to 30 animals) Trichoptera percentages have decreased with increased fauna percentages, there have been compensating changes in the Mollusca (also a hard-case group), and it is possible that larger samples would indicate a correlation. However, in all the data, the Ephemeroptera is the only group to show any correlation with fauna changes.

The eels exercising selection are also apparently affected by faunistic differences. In area I a higher percentage of Ephemeroptera and a lower percentage of Trichoptera is taken by those selecting, and in areas III and IV the reverse occurs. From these limited data it seems that selection of one particular animal is not entirely due to food preferences of the eel. It may be to some extent a tendency to feed on one type of animal, with the choice of animal determined by its relative abundance in the fauna.

TABLE 14

STOMACH CONTENTS OF WAINUI-O-MATA R. EELS

Class of Animal	No. of Animals Present	Area I		Areas III and IV	
		Under 24 in.	Over 24 in.	Under 24 in.	Over 24 in.
Trichoptera	<30	21.8%	50.4%	11.6%	27.1%
	>30	6.5%	39.0%	47.4%	83.5%
Ephemeroptera	<30	68.5%	19.1%	40.2%	10.2%
	>30	83.2%	41.6%	8.3%	0.8%
Coleoptera	<30	—	—	11.6%	3.4%
	>30	0.1%	—	9.6%	2.9%
Diptera	<30	9.7%	12.2%	4.5%	17.0%
	>30	10.6%	16.9%	0.1%	0.2%
Neuroptera	<30	—	—	—	—
	>30	0.06%	—	—	0.2%
Odonata	<30	—	—	6.2%	—
	>30	—	—	—	—
Crustacea	<30	—	0.9%	13.4%	5.1%
	>30	—	—	1.2%	0.01%
Mollusca	<30	—	16.5%	6.2%	33.9%
	>30	0.06%	2.6%	32.6%	12.2%
Terrestrial	<30	—	0.9%	6.3%	3.4%
	>30	0.06%	0.3%	1.0%	0.01%
Number of stomachs examined	<30	12	5	10	6
	>30	23	3	8	19
Number of animals found in each sample	<30	206	115	112	59
	>30	1672	313	982	6228

Further data for comparison of the effects of the bottom fauna variations are given in Table 15. For this table all stomachs were combined, irrespective of the number of animals in them. It can be seen that in the shingle-bed rivers, the Lillburn, Wainui-o-mata, and the Whitestone, over 75 per cent. of the stomach contents are provided by two groups, the Trichoptera and Ephemeroptera. As there is only a small number of stomach samples, and it has been found since that insufficient faunistic samples were taken to give accurate figures, a detailed study of the correlation between the stomach contents and the bottom fauna has not been attempted. There are, however, indications that the Ephemeroptera percentages vary with bottom fauna densities.

TABLE 15

STOMACH CONTENTS OF EELS TAKEN IN BAITED TRAPS

Food	Lillburn R.			Wainui-o-mata R. (Area I)			Whitestone R.			Wainui-o-mata R. (Areas III and IV)			Waipa R. Stomach Contents (%)	Kaniwhanawhana R. Stomach Contents (%)
	Bottom Fauna			Bottom Fauna			Bottom Fauna			Bottom Fauna				
	No. of Animals/ sq. ft.	Percentage	Stomach Contents (%)	No. of Animals/ sq. ft.	Percentage	Stomach Contents (%)	No. of Animals/ sq. ft.	Percentage	Stomach Contents (%)	No. of Animals/ sq. ft.	Percentage	Stomach Contents (%)		
Trichoptera	55	14.8	71.3	139	22.1	42.0	157	21.3	69.8	169	48.3	83.0	6.2	24.5
Ephemeroptera	69	18.5	7.6	152	24.2	35.5	91	12.3	17.2	10	2.8	0.9	—	16.4
Plecoptera	—	—	0.3	—	—	—	0.5	0.07	10.3	1	0.3	—	—	—
Coleoptera	206	55.6	0.3	146	39	—	467	63.6	0.2	132	37.6	3.0[a]	—	—
Diptera	34	9.2	3.6	84	13.4	15.7[b]	20	2.7	0.4	29	8.3	0.4	—	—
Neuroptera	3	0.7	6.7	0.25	0.04	—	0.5	0.07	—	1	0.3	0.2	0.7	—
Odonata	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—
Crustacea	—	—	10.0	0.25	0.04	0.5	—	—	0.2	1	0.3	0.6	15.0[c]	38.5[d]
Mollusca	4	1.1	—	7	1.1	6.3	—	—	—	6	1.7	12.4	41.8	1.6
Oligochaeta	0.5	0.1	[e]	—	—	—	1.5	0.2	—	—	—	—	—	—
Miscellaneous	—	—		1	0.2	0.5	—	—	2.0	2	0.6	0.1	34.8[f]	18.0
No. of Animals	—		329			428			525			6287	406	61
No. of Stomachs	—		10			9			27			29	74	27
No. of Faunistic samples	4			4			4			5				

[a] 95% Parnid imagos. [b] 72% Chironomidae. [c] Includes 32 *Paranephrops* — each equivalent to several thousand other animals. [d] Includes 7 *Paranephrops*. [e] Treated separately — see text. [f] 80% Bees (Apidae).

While it can be said that the eel has some preferences, its feeding habits are generalized and readily adaptable to most faunistic differences. This adaptability is illustrated in Table 15 by the stomach contents of eels taken in rivers of a markedly different type from those already discussed. In both the Waipa and the Kaniwhanawhana the most important item in the diet when considered in terms of weight is the freshwater crayfish (*Paranephrops* spp.).

Studies on the feeding habits of the European eel (*Anguilla anguilla*) by Frost (1946) and Hartley (1948) agree in general with the results obtained by the author. Detailed comparisons are not, however, possible as neither of these authors gives data on the bottom faunas of the rivers or lakes from which their specimens were taken.

Although animals of terrestrial origin have not yet been discussed, it is thought that they may play an important part in the diet of eels. The sample of eels from the Lillburn, taken three days after a fresh, contained 89 per cent. (dry weight) animals of terrestrial origin (mainly worms and caterpillars). A similar occurrence of worms in the eel stomach contents was seen in eels taken shortly after a fresh in the Lower Whitestone River. Also in the Lillburn area two lagoons were trapped during a fresh when a considerable area of normally dry land was covered with water. All the eels caught during this period had large quantities of worms, caterpillars, etc. in their stomachs, and entered baited traps freely during the day as well as at night. This daylight trapping would appear to indicate an abnormally high feeding intensity as it was not effective in the river during this period or in these lagoons when the water level had returned to normal. It does appear probable that, in areas where conditions are suitable, animals of terrestial origin washed into the streams could play an important part in the food of eels.

(*b*) *Predation on Fish*

In Table 16 the occurrence of fish in stomach contents is shown. The main conclusion that can be drawn from the facts is that there are two groups of streams, with large differences in the degree of predation. Two different types of waters are represented, the first four rivers having open shingle beds and the last two being stable with weed bottoms. It is possible that the streams with a higher predation rate have also a larger young trout population, but it is not thought that it would be sufficiently different to account fully for the higher predation rate.

It may be that in the weed the eel has a much better chance to capture trout. It must be remembered that the above data are not fully quantitative, and it is necessary to make a number of assumptions to give any estimate of the numbers of trout eaten by eels.

In Table 17 the Kakapo and Flaxy results have been combined and split up into size groups. It can be seen that the tendency to take trout increases with the size of the eel, with no eels of less than 28 in. taking trout. There is also some indication of a tendency for the number of trout taken per eel to increase with size. This agrees with the interpretation already given of the shape of the length frequency curve for trapped eels (Fig. 4*B*). It would thus appear that carrion-feeding tendencies are strongly developed in the larger eels. While only a few instances of carrion (other than bait) have been observed in the stomach contents, eels in the traps frequently had some, and occasionally all the carrion bait in their stomachs. Schiemenz (1910), quoted by Frost (1946), maintains that the European eel does not feed on carrion.

TABLE 16

EELS TAKEN IN BAITED TRAPS

River	Eels Examined (No.)	Eels With Trout (No.)	Eels With Trout (%)	Trout (No.)	Trout per Eel	Eels in Stomach Contents
Wainui-o-mata	169	2	1.2	2	1.0	2
Whitestone (upper)	54	1	1.9	1	1.0	—
Whitestone (lower)	97	2	2.1	2	1.0	—
Ngakoaohia	41	1	2.4	1	1.0	—
Kakapo	132	25	18.9	60	2.4	—
Flaxy (lower)	28	13	46.5	27	2.1	—

TABLE 17

TRAPPED EELS: KAKAPO AND FLAXY STREAMS

Length of Eel (in.)	No. of Eels	Eels Containing Trout (No.)	Eels Containing Trout (%)	No. of Trout	Trout per Eel
20-24	2	—	—	—	—
24-28	22	—	—	—	—
28-32	60	12	20.0	22	1.8
32-36	55	16	29.1	39	2.4
36-40	14	5	35.7	15	3.0
40-44	7	5	71.4	11	2.1

The mean length of all the trout was 3.5 in. and the largest found was 6.25 in. All the fish taken were thus in their first year and it is important to remember this when considering predation effects. Cairns (1942*a*) found salmonids in 1 per cent. of the eels trapped in the Hedgehope river, but gives no data on the size of the salmonids found. Cairns also shows that very few trout of less than 12 in. long are eel-scarred. From this he concludes that eels are capable of swallowing whole trout of up to 12 in. in length. The occurrence of trout can also be examined in terms of weight. For the Wainui-o-mata River trout made up approximately 5 per cent. by wet weight of the food. This can only be used, however, when data are available on the total food requirements of eels.

It is desirable that feeding experiments be done as a check on the results obtained by any method. In the present experiments the stomachs (excluding empty ones) contained on the average food of 0.12 and 0.15 per cent. of the body weight of the fish (Table 13). This would appear to be much lower than the usual figures given for 24 hours' food requirements. For this reason an attempt has been made to estimate the total food requirements, using data from quantitative feeding experiments done with other fish.

VII. Estimated Total Food Requirements

When growth requirements and maintenance requirements are presented separately, an approximation of the total requirements can be made, using data obtained for other fish.

(*a*) *Maintenance Requirements*

Ricker (1949) gives a daily maintenance ration value of 1.7 per cent. of the body weight for bluegills (*Lepomis macrochirus*) over a range of from 33 to 56 g. Dawes (1931) gives a comparable figure for plaice (*Pleuronectes platessa*) of the same size but shows that maintenance requirements vary with the size of the fish. The maintenance ration for plaice of 135 g. weight was approximately 1 per cent. of the body weight per day. Brown (1946) gives a very similar maintenance requirement curve for brown trout. Pentelow (1939) found for brown trout no evidence of variation with size, and obtained a general maintenance requirement of 1.2 per cent. of the body weight per day.

There are two difficulties in deriving a likely figure for eels; firstly the eels under consideration are much larger (1.31 kg. mean wt.) than the fish used in these experiments and, secondly, the eel is probably a less active fish. However, it would probably be safe to assume that 1 per cent. is the maximum maintenance requirement for eels of the size being considered.

(*b*) *Growth Requirements*

In order to estimate the growth requirements it is necessary to know the net efficiency of conversion of food to body weight. The net efficiency is the amount of food available for growth (i.e. the total food eaten, less the estimated maintenance requirements) divided by the increase in weight. The values for net efficiency of conversion obtained by Dawes (1931), Ricker (1949), and Pentelow (1939) agree remarkably well, as shown in Table 18.

For the purpose of this estimation an efficiency of conversion of 4 g. of food to 1 g. of growth has been assumed. The growth rate has been

TABLE 18

NET EFFICIENCY OF CONVERSION

Author	Fish	Food	Food (g.)/Growth (g.)
Dawes (1931)	*Pleuronectes platessa*	*Mytilus edulis*	Approx. 5
Ricker (1949)	*Lepomis macrochirus*	Earthworm	4.4
Pentelow (1939)	*Salmo trutta*	*Gammarus pulex*	3.35

calculated from data presented by Cairns. It was found that, for all practical purposes, log length was linearly related to log age over the range of sizes being considered (Fig. 8). The age-weight relationship can from this be expressed as

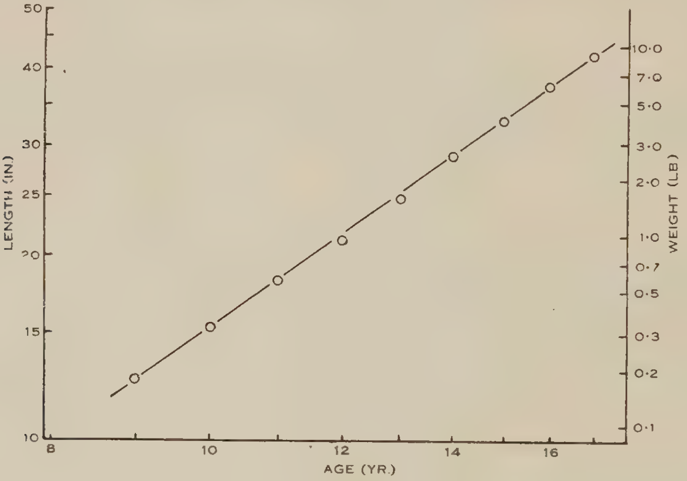


Fig. 8.—Cairns's (1941, 1942*a*, 1942*b*) data on the age of eels can be expressed as a linear log length: log age relationship for the size range being considered. The formula thus obtained is used for the determination of growth rates at various sizes.

$$W = T^{6.33} \times 10^{-6.817},$$

where W = weight (lb.), and T = age (yr.).

Then log rate of increase $= \dfrac{d \log W}{dt} = \dfrac{6.33}{t} \times 0.4343.$

Assuming that the active period of an eel is spread over 230 days in the year, then daily rate of increase = antilog $\left(\dfrac{6.33}{t} \times \dfrac{0.4343}{230}\right)$.

From this formula it can be seen that the percentage daily rate of increase in weight decreases with increasing size. If this rate of increase is then multiplied by the food to growth conversion factor (4) and added to the maintenance requirements, the resulting figure is the total daily food requirements expressed as a percentage of the body weight. In Table 19 a number of examples have been worked out. In Table 20 the theoretical requirements are compared with the actual weight of animal found in the stomach contents.

TABLE 19

THEORETICAL FOOD REQUIREMENTS

Weight of eel (kg.)	0.1	0.28	0.6	1.31	3.0
Daily increase in weight (%)	0.29	0.26	0.22	0.19	0.17
Daily increase × 4.0	1.16	1.04	0.88	0.77	0.68
Maintenance requirements	1.00	1.00	1.00	1.00	1.00
Total requirements (% of body wt.)	2.16	2.04	1.88	1.77	1.68

There are a number of factors which may account for the disparity between the calculated requirements and the practical results. It does not appear to be due to a high rate of digestion, or turnover in the stomach. Cairns (1942*a*) found that food remained in the stomach for from 24 to 36 hours. The author conducted a similar experiment in which eels known to be feeding were captured, placed in a trap in such a way that they could not feed, and examined at intervals. It was found that, under these circumstances, the food remained in the stomach for at least 33 hours. Digestion of insects would appear to take at least 24 hours. The stomach is capable of considerable distension, and as the eel probably feeds only during part of the night, it is thought probable that the food ingested during the night remains in the stomach for most of the following daylight hours. The intestine is short and capable of holding very much smaller quantities than the stomach.

TABLE 20

COMPARISON OF ACTUAL FOOD FOUND WITH THEORETICAL REQUIREMENTS

Type of Catch	No.	Mean Weight	Food Found (% of body wt.)	Calculated Requirements (%)	Calc. Req. / Food Found
Gaffed	55	0.28 Kg.	0.15	2.04	13.6
Trapped	49	1.31 Kg.	0.12	1.77	14.75

* Eels without food in stomachs are not included for calculation of this figure.

It would thus appear that the amounts of food found in the stomachs were representative of the quantities actually present at the time of capture. However, with the trapped eels, the time of capture is not known and it is probable that the bait used attracts the eels from their normal feeding. The gaffed eels were taken mainly between 10 p.m.

and midnight, and thus their feeding time was probably curtailed. The next step is to obtain a sample of eels as soon as they have finished feeding (i.e. in the early morning). Owing to their habits, this is very difficult with methods of capture at present available. It will be necessary to investigate other methods, of which the use of electricity appears to be the most suitable.

There is also the possibility, already discussed, that eels obtain part of their food requirements from large, intermittent meals of animals of terrestrial origin.

VIII. Conclusions

The baited trap has a maximum range of about 100 yd. For 90 per cent. removal of trappable eels the least effort is required for sets at approximately 67 yd. spacing.

Trappable population densities of between 30 and 1,358 lb./ac. were found in rivers of various types throughout New Zealand. The density of the eel population is apparently limited by the amount of cover present.

The length frequency curves for the two methods of capture used show two changes in habit. First there is a change from a cryptozoic way of life when about 12-14 in. long, and second the appearance of carnivorous tendencies, apparently fully developed when the eel is 30 in. long. Also, the tendency to take trout first appears when the eels are about 28 in. long, and increases in intensity with increasing size of the eel.

The shape of the length frequency curve for trapped eels indicates that trapping would need to be repeated every third or fourth year in order to keep a stream clear of the larger eels. The smaller (less than 24 in.) eels, which are possible competitors with the trout for food, are only occasionally caught by the use of carrion-baited traps.

The feeding habits are generalized and adaptable to most faunas. In the shingle-bed streams examined, 75 per cent. of the stomach contents was made up by Trichoptera and Ephemeroptera larvae.

Trout occurred frequently only in the stomach contents of eels from streams with heavy weed beds. The mean length of all the trout found in eel stomachs was 3.5 in.

The methods of capture used make the results obtained unsuitable for fully quantitative studies on feeding habits. It is thus not possible to make any estimates of predation or competition effects from the data so far collected.

Further investigation of the feeding habits is necessary along lines indicated by the present investigation. Interpretation of these data would require a knowledge of the bottom-fauna production and also the production of trout.

IX. Acknowledgments

The author wishes to thank Mr. K. R. Allen for helpful discussion and criticism throughout the work and also during the preparation of the

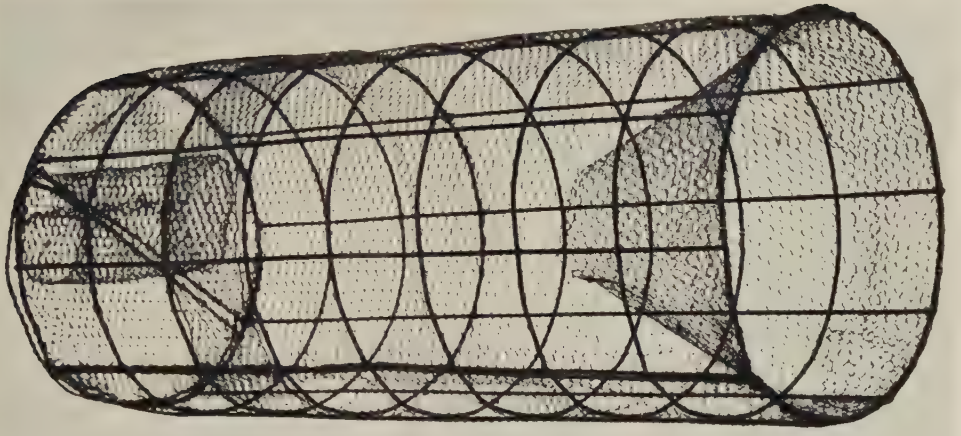


Fig. 1.—The type of eel trap used in this investigation. The framework was constructed from sheet reinforcing (7/32 in. rod). This was covered with galvanized wire netting, preferably of 1 in. diameter mesh.

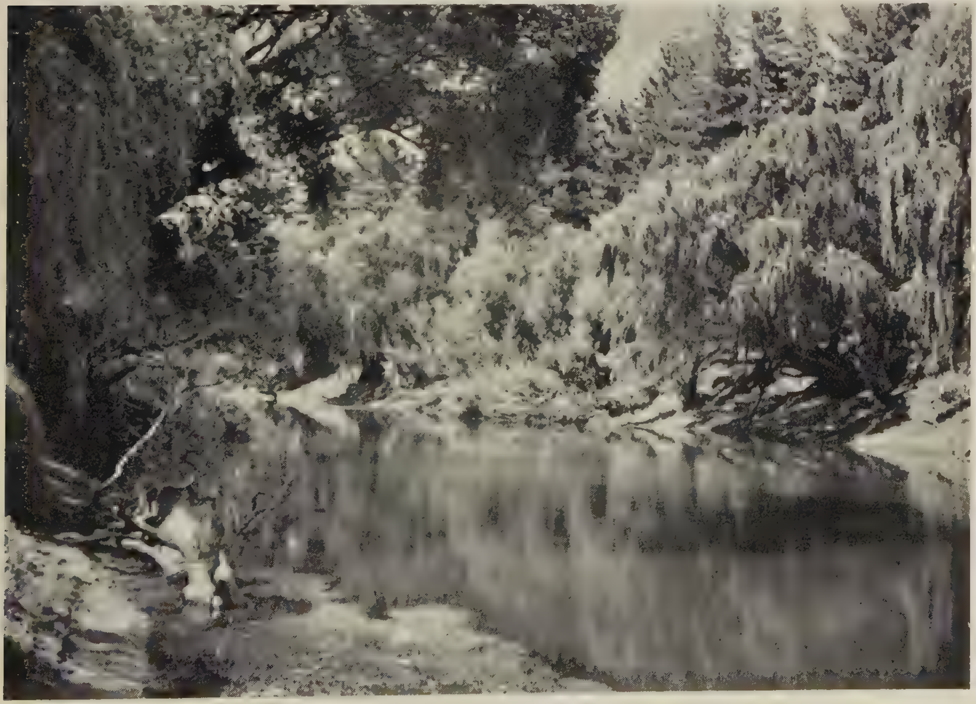
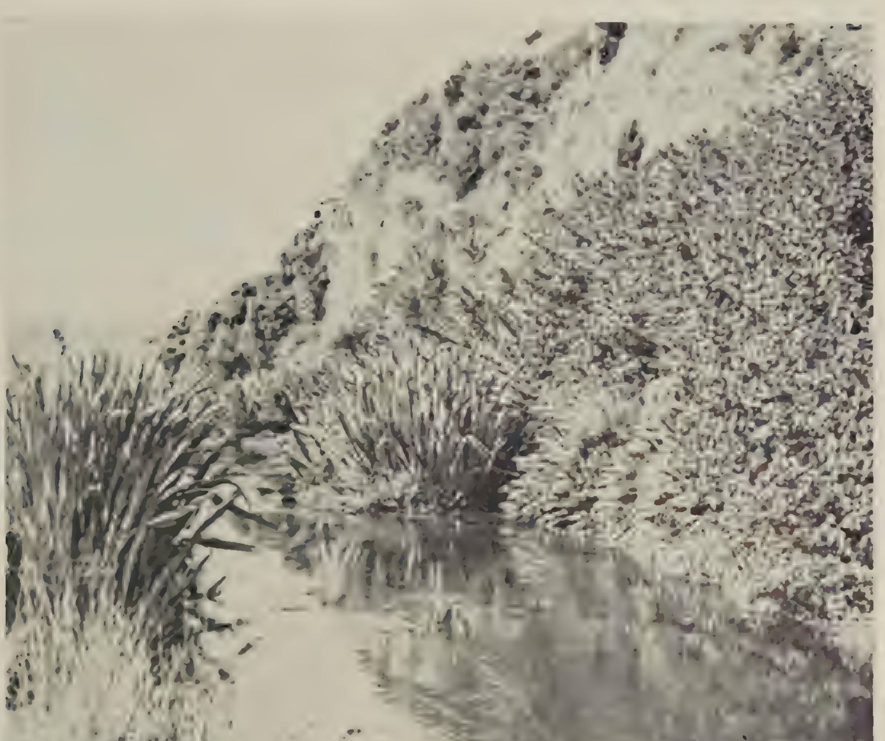


Fig. 2.—The Waipa River, Waikato District—a stable, sluggish, deep river with slightly turbid water which provides good eel cover. Yield 275 lb./ac.



The Kakapo Stream in Southland—a stable, heavily weeded stream with overhanging banks and thus plenty of cover for eels. A yield of 1,358 lb./ac. was obtained.

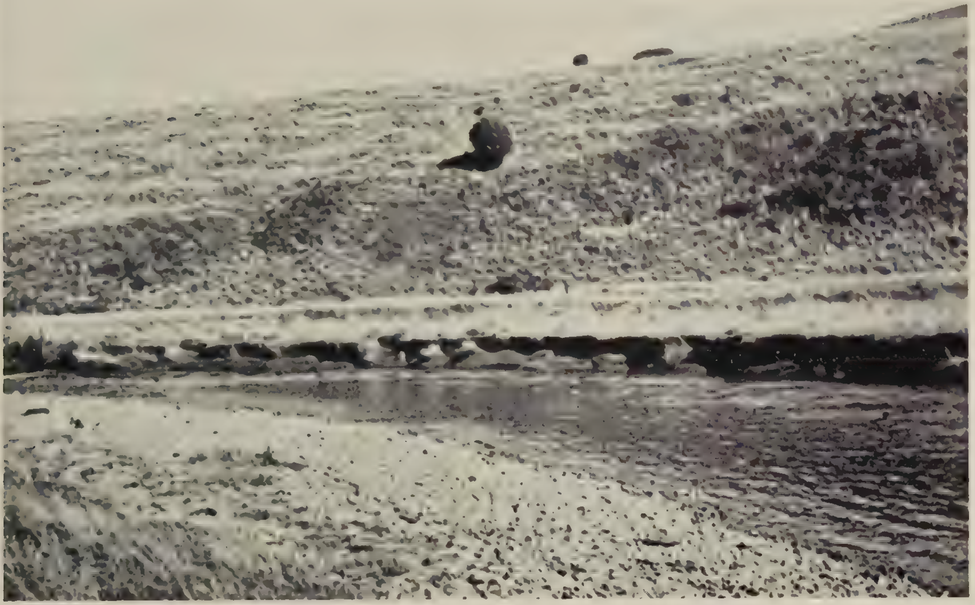


Fig. 1.—The lower Whitestone River in Southland—a moderately stable stream with a shingle bed and varying amounts of cover. The section of fallen sod bank illustrated gave a yield of 98 lb./ac.

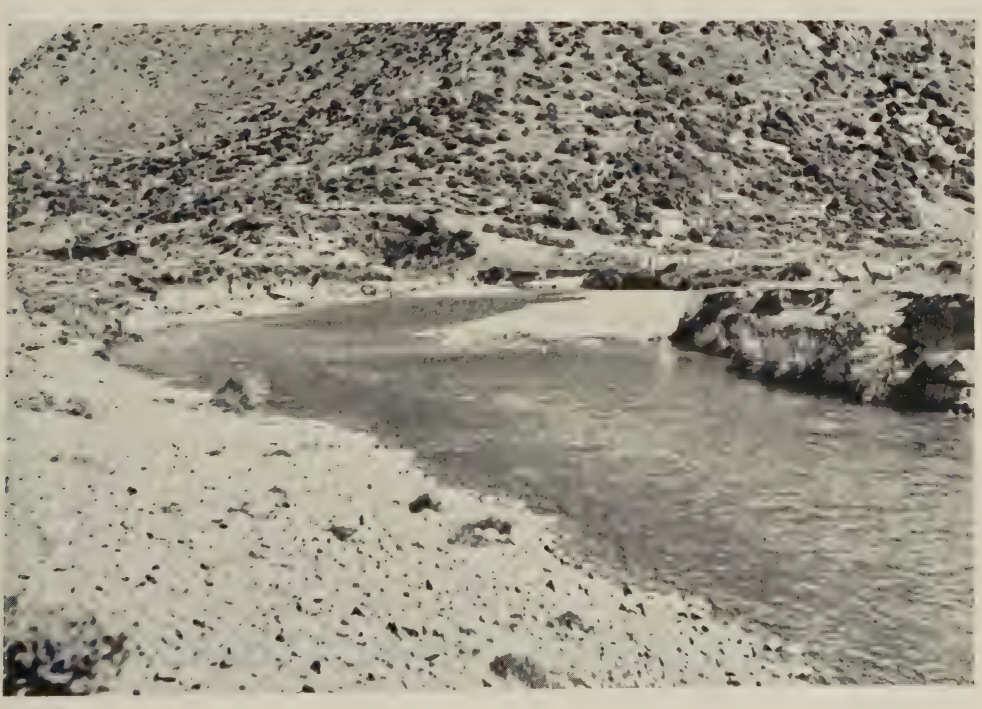


Fig. 2.—The Wainui-o-mata River, Wellington—a moderately stable stream with a shingle bed and little cover other than pools. The section of very open water illustrated yielded 14 lb./ac.

manuscript; Mr. D. F. Hobbs for much useful information and also for permission to use unpublished data; the Southland Acclimatization Society for assistance while working in their district; the members of the staff of the Fisheries Research Laboratory, who have assisted with the work in the field and in the laboratory; and the Department of Internal Affairs for details of eels caught in the Southern Lakes district.

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THE ACCLIMATIZATION AND GROWTH OF THE PACIFIC OYSTER (*GRYPHAEA GIGAS*) IN AUSTRALIA

By J. M. Thomson*

(*Manuscript received August* 17, 1951)

Summary

A trial shipment of Pacific oysters, *Gryphaea gigas* (Thunberg), natives of Japan, was brought to Australia in 1940. The shipment was condemned on arrival. Successful shipments were made in 1947 and 1948. The stock set out in Oyster Bay, near Albany, Western Australia, failed to survive the first winter, but those in southern Tasmania thrived. Growth rate was similar to that shown by the species on the west coast of North America. A slight spat-fall occurred in the summer of 1949-50 and a heavier one in 1950-51. It is doubtful if this is sufficient to replace the parent stock. An augmented brood stock is probably needed.

I. Introduction

As early as 1939 the recently formed Division of Fisheries of what is now the Commonwealth Scientific and Industrial Research Organization was considering what could be done to increase the area under oyster cultivation in Australia. The mud or Port Lincoln oyster, *Ostrea angasi* Sowerby, once common along the southern coast, had been overfished during the 19th century and attempts by various private and governmental agencies to farm it had failed. The Sydney rock oyster, *Gryphaea commercialis* (Iredale and Roughley) of the eastern coast had been taken to South Australia, Western Australia, and Tasmania without becoming acclimatized. The southern States are outside the natural range of this oyster, which does not exist naturally very far south of the border between Victoria and New South Wales.

Consequently it was decided to attempt the importation of the Pacific oyster, *Gryphaea gigas* (Thunberg) which has been imported so successfully on the west coast of North America (Elsey 1934; Anon. 1940).

II. The Shipments

Owing to an error in trade circles in Japan, where an enquiry regarding supplies of spat was mistaken for a definite order, a shipment of seed oysters was sent to Australia in 1940. This was consigned as deck cargo as is usual in the trade with North America. However, the voyage to Australia is much longer and also across the tropics. The conditions were too severe and the shipment was condemned on arrival in Sydney.

Further plans were halted until the end of the war in the Pacific. Then two shipments were brought out, one in November 1947 and one in November 1948. This time of year was selected since temperatures in the two countries are then comparable, and also since summer growth then commences in Australian waters.

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In order to make sure that the oysters received the best possible attention, an officer of the Division went to Japan beforehand to inspect the oysters on the seed beds and during packing and to tend them on the voyage to Australia.

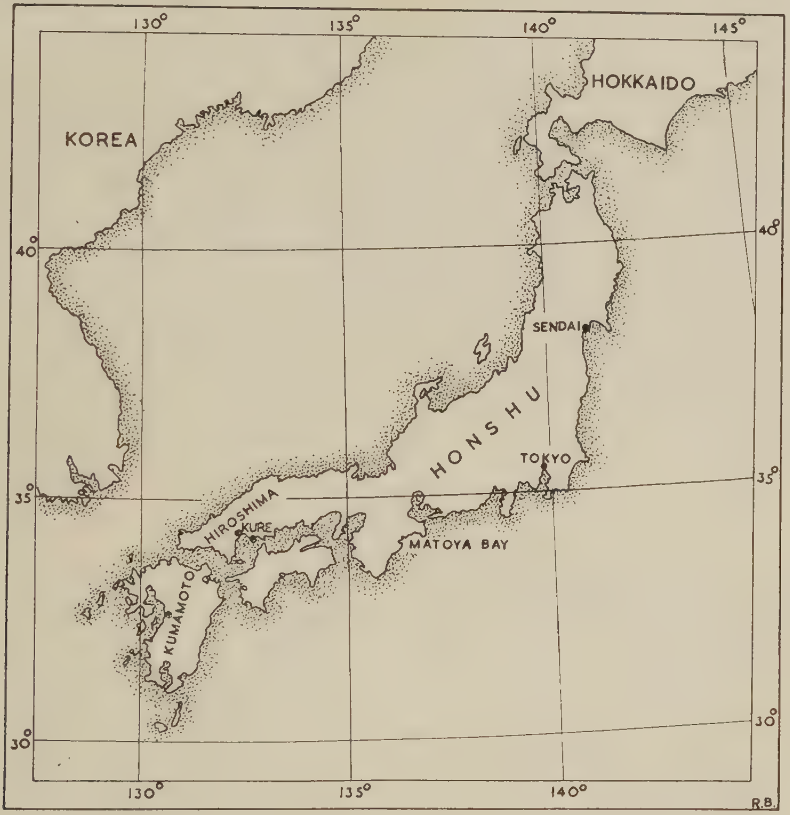

Fig. 1.—Japan, showing oyster grounds mentioned in the text.

Fifty-five cases of seed oysters were brought out to Australia in 1947. Fifty of these came from near Sendai, a big oyster-producing area about 100 miles north of Tokyo (Fig. 1), whence the pre-war American stocks had been obtained. The other five cases came from Kumamoto on the west coast of the southernmost of the three main Japanese islands. In 1948, 50 cases of oysters were brought from Hiroshima, which has the advantage of being near the shipping point of Kure.

Each case of oysters contained a minimum of 15,000 seed oysters, caught upon old oyster and scallop shells. No cultch shell was included unless carrying at least 15 seed oysters in the Sendai oysters, or 10 seed oysters in the lot from Hiroshima, the cultch shells from the latter centre being smaller than those used at Sendai.

En route to Australia, the seed oysters were held in fruit lockers at a temperature of 50°F. in order to avoid the fierce heat of the tropics. The cases were hosed down daily to keep them moist. A few cases were opened daily in order to time and check the intensity of any mortality.

From Sydney, which is a considerable distance from the sites chosen as suitable test areas, the 1947 shipment was sent on by air; the 1948 shipment was transferred to a divisional research vessel for delivery.

III. The Acclimatization Beds

After studying what information was available, both from Japanese and American sources, on the ecology of *G. gigas* (Amemiya 1921, 1928; Chapman and Esvelat 1943; Elsey 1932, 1934; Fujita 1929; Galtsoff 1932; Hatai 1929, 1934; Holway 1934; Hopkins 1935, 1936; Ishida 1935; Quayle 1940; Schaeffer 1938; Seno, Hori, and Kusakabe 1926; Wakiya 1929; Willapoint Oyster Growers' Association 1932), two sites were chosen as test acclimatization areas. One of these was at Oyster Harbour in south-western Australia and the other at Pittwater in Tasmania (Figure 2).

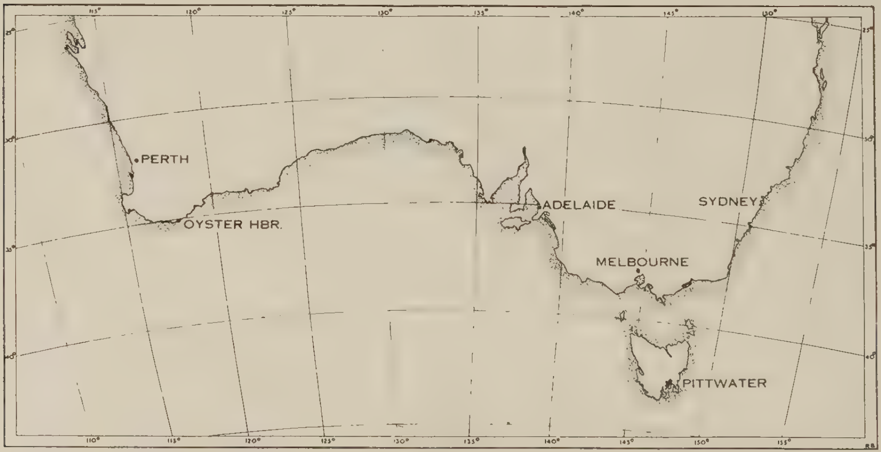

Fig. 2.—Southern Australia, showing Pittwater and Oyster Harbour.

(*a*) *Oyster Harbour*

Oyster Harbour is about three miles long, two miles wide, and has a sandy and rock bottom. The maximum depth is about 18 ft., but the average is much less, considerable portions being only about 2 ft. deep. In common with other south-western Australian estuaries there is practically no tide. The Harbour opens to King George's Sound by a narrow opening about 100 yd. across. Two rivers, the King and the Kalgan, enter Oyster Harbour at its upper end. These run through poor country and are not rich in nutrients. They are not long rivers, the King being only 25 miles long and the Kalgan about 60 miles.

Two beds were set out in Oyster Harbour. One was in the centre in about 12 ft. of water, in which wire trays were suspended at various depths from near the bottom to the surface. The other bed was on the foreshore about half a mile from the entrance of the King River into the Harbour. Here the oysters were put on wire trays supported a few inches above the bottom in 2 ft. of water. Other oysters were scattered on firm bottom adjacent to both beds.

(*b*) *Pittwater*

Pittwater is an irregularly shaped inlet about 10 miles in length with a width varying from two miles to a quarter of a mile. The Cole River enters at the upper end and several creeks enter at various places. There are extensive areas of shallow flats with an average depth of 2-4 ft. Depths up to 30 ft. are found in the channels. Although the opening to the sea is narrow, there is a marked tide of 3-4 ft., masked at times by the piling up of coastal waters by continued southerly winds.

At the spot chosen for the oyster beds the shallow flat extends for about 400 yards from the shore before reaching the deep channel, into which it dips sharply. Three groups of trays were set out, one close inshore, one half way out, and one near the edge of the channel. Other oysters were scattered on the bottom, which is of fairly firm, muddy sand.

IV. Rate of Survival

(*a*) *During Transhipment*

The oysters were out of water approximately 20 days en route from Japan to the test beds. No deaths were apparent during the first seven days. After that a few gaping oysters were noted each day but they remained few in number until the sixteenth day, when a distinct increase in the number of dead oysters was noted and after which more oysters died each day. On arrival of the spat at the setting-out beds, it was estimated, on the basis of the number of shells gaping, that 60 per cent. of the oysters had survived the trip. The Sendai and Hiroshima oysters survived somewhat better than those from Kumamoto.

(*b*) *In Australia*

A week after setting out it became evident that not only were the gaping oysters dead but many of those that were still closed were moribund, failing to recover when set out. From counts it appeared that about 50 per cent. of the oysters that appeared to be alive when set out failed to recover. In other words, only 30 per cent. of the seed oysters that left Japan lived when the consignment was set out in Australian waters.

From this stage on the history of the Western Australian samples differed from those in Tasmania. In Oyster Harbour, numbers declined at first sharply, then more slowly but steadily, whereas the oysters in Pittwater showed practically no mortality for several months, after which deaths slowly increased, as is to be expected in any natural population.

Those oysters set out near King River were all dead by February 18, 1948. After the winter of 1948, no live Pacific oysters could be located in Oyster Harbour but they survived with little loss in Pittwater (Table 1). These figures refer to the 1947 shipment. The survival rate of the 1948 oysters sent to Tasmania was similar.

TABLE 1

SURVIVAL RATE OF PACIFIC OYSTERS

During Transportation		After Setting Out		
Days from Japan	Percentage Alive	Days from Japan	Tasmania	W.A.
1	100	27	30	30
7	100	40	30	15
8	98	70	25	12
10	96	100	25	8
12	92	130	25	8
14	90	200	25	0
16	78	300	18	
18	70	400	18	
20	60	700	10	
		1000	8	

There are two hypotheses that may be advanced to explain the failure of the acclimatization attempt in Western Australia. Firstly, there is practically no tide there and it may be that there was simply not enough food material conveyed to the oysters. Secondly, a heavy growth of algae, principally *Enteromorpha*, occurred in Oyster Harbour in 1948 and the

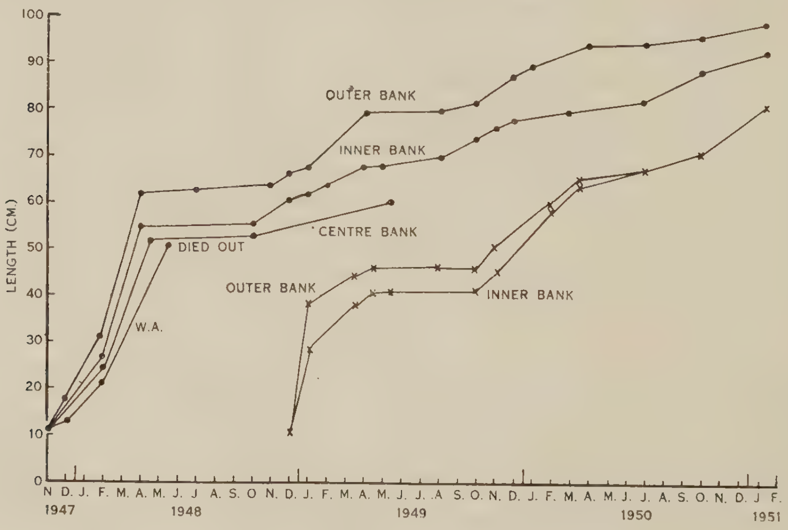

Fig. 3.—Increase in length of 1947 and 1948 oysters.

final deaths coincided with the decay of the algae, which may have emitted toxic substances in this condition. There are no other obvious features of the environment that may have affected them. Temperatures in Oyster Harbour were above those in Pittwater but this should have increased the feeding rate and thus been beneficial rather than otherwise.

V. Growth

Growth over the first year was extremely rapid, the mean increase in length being six times the size at setting out. The rate of growth in all dimensions decreased in later years. Individual growth varied widely; thus although the mean length at the end of three years was 9.4 cm., the size range extended from 6 cm. to over 15 cm. At Pittwater some variation was shown according to the position of the bed (Fig. 3). Those oysters on the outer edge of the flat, that is nearest the deep water channel, grew at the fastest rate. However, those half way out along the flat did not grow as fast as those closest in. The mid-flat region is a level area where tidal flow is reduced. But there is a minor tidal channel running along the inshore edge of the flat at this point. During the winter of 1949 the centre trays were washed away in a gale. As growth in that position had

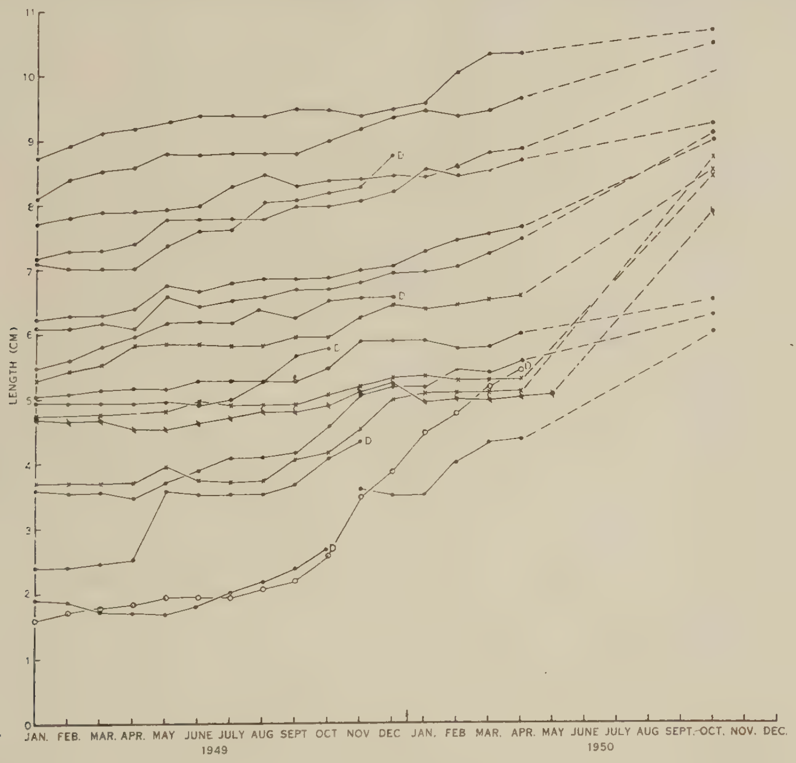

Fig 4.—Seasonal growth of individual oysters (*D* signifies death of the oyster).

proved to be slower than elsewhere on the flat, the oysters recovered were set out amongst the outer trays.

The seasonal growth curves are typically sigmoid, growth slowing down in winter and accelerating in summer. However, not all the oysters stopped growing over the winter period as is shown for individual oysters that were kept in compartmented trays, one oyster to each compartment (Fig. 4).

Weekly readings of temperature were taken on maximum-minimum thermometers set out on the oyster beds. It appears (Fig. 5) that it is the minimum temperature that is important, as the maximum temperature had risen appreciably for some time before general growth recommenced coincidentally with a sudden rise in the minimum temperature.

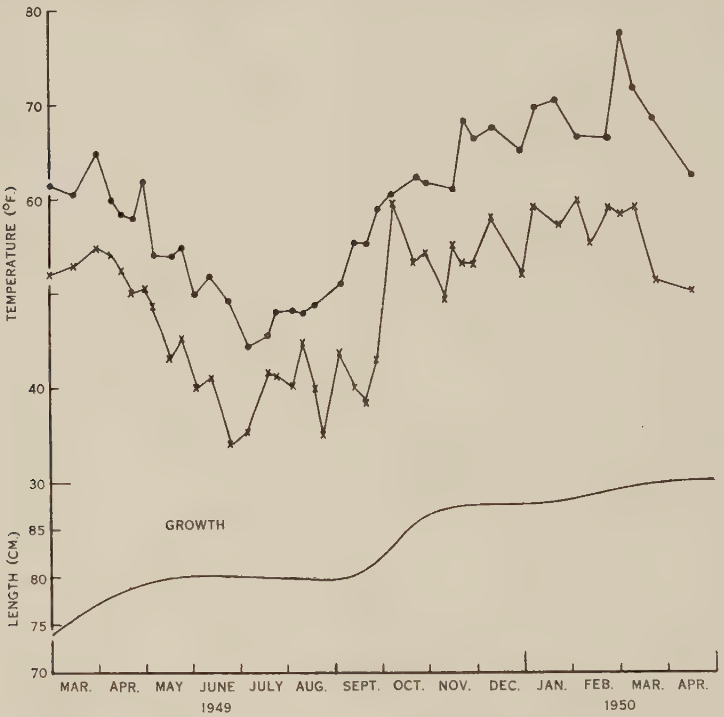

Fig. 5.—Seasonal growth compared with maximum and minimum weekly temperatures.

It will be noted (Fig. 4) that at times a diminution in length is recorded. A proportion of this may be due to errors in measurements, but reduction often results from breakage of the thin-lipped edge of the shell during handling. Loosanoff and Nomejko (1949) have already drawn attention to this source of error in estimating oyster growth.

The cumulative monthly growth curves show certain differences from those found by Loosanoff and Nomejko (1949) for *Ostrea virginica*. As mentioned above, some individuals showed active growth even when subject to the lowest temperatures of the year in June, July, and August. However, these were exceptional and the general tendency was to cease growth during June and July. Increase in depth and width commenced in August, but increase in length was not detected until September (Fig. 6). This differs from the finding of Loosanoff and Nomejko for *O. virginica* where increase in length and width was noticeable in spring, but depth increase did not occur until late summer. These curves are constructed from mean figures and individual time of growth varies (Fig. 4).

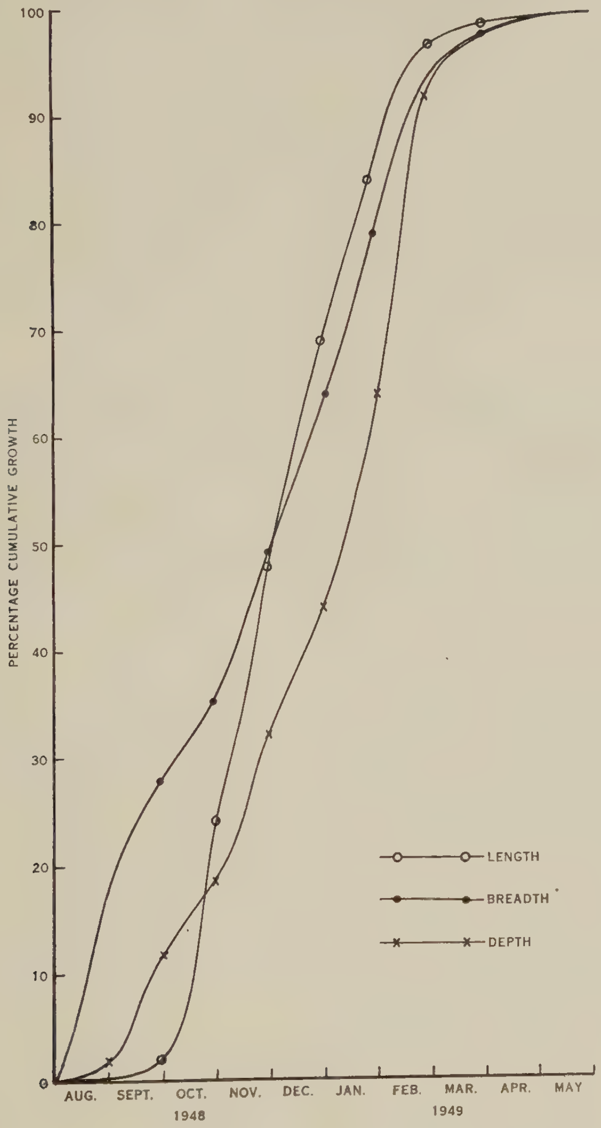

Fig. 6.—Cumulative seasonal growth in different dimensions.

There is little published information upon the size attained each year by *G. gigas* either in Japan or America. Galtsoff (1930) reports four-year-old oysters at Samish Bay measuring "about 13 cm. in length and 7 cm. in width". He figures an oyster of the same age that measured 11 × 8.4 cm. According to Elsey (1933), *G. gigas* in British Columbian waters grows to a length of 11-15 cm. in two to four years. Growth of the Tasmanian oysters is satisfactory on these standards as after three years they measure from 6 to 15 cm. in length.

There is a statement (Sato 1948) that in the first month after setting the oysters in Matoya Bay, central Japan, grow 1 cm. At five months they are 4.5 cm. and at nine months they are 10 cm., which is much faster growth than shown in either Australian or American results, and needs to be reliably tested before being accepted. According to Wakiya (1929) this species "at the age of two years . . . is no more than 12 cm.".

VI. Reproduction

From visual inspection of oyster meat samples taken fortnightly it can be stated that spawning occurred during early February in 1949 and 1950 and during mid January 1951, in each case when the water temperature had risen above 22°C. The summer of 1949 was particularly cold and little spat settlement occurred. Rather more spat was evident from the 1950 settlement. The temperatures during the summer of 1951 remained high for an unusually long duration and the spat catch seems to be better than in the previous years.

VII. Conclusions

The Pacific oyster (*G. gigas*) has been successfully transferred to a southern hemisphere environment. From the mortality rate during transit it appears that a high rate of survival is possible by reducing the duration of the trip from Japan to Australia to less than 14 days, which would have been possible under pre-war shipping conditions. The oysters have grown well in Pittwater (Tasmania), have spawned, and have provided a set of spat. However, the density of the fall was not great and an enlarged brood stock may be necessary in order to achieve a rapid increase in the population. A possible alternative is the development of a spatting tank technique such as Cole (1938) and Imai, Hatanaka, and Sato (1950) have achieved on an experimental scale.

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A PRELIMINARY STUDY OF THE LIMNOLOGY OF LAKE HAYES

By VIOLET H. JOLLY*

(*Manuscript received March* 8, 1951)

Summary

A general description is given of Lake Hayes, a freshwater lake in the South Island of New Zealand, with a brief analysis of its physical conditions.

Preliminary samplings from a variety of lakes showed that Lake Hayes possesses a comparatively rich zooplankton, noteworthy for the fact that its bulk is made up of few species, chiefly entomostracan Crustacea. The greatest number of organisms occur in the upper 6 fathoms but there is a vertical distribution through the complete range. Seasonal fluctuations are marked, the phytoplankton showing greatest productivity in spring, while summer and autumn peaks are dominated respectively by cladocera and copepods.

The Entomostraca manifest a diurnal vertical migration. There is a concentration of the population in the surface waters at dawn and dusk. During the day, the migrants desert the upper waters, while at night the numbers assume average proportions but no peak periods occur. It appears that the Entomostraca of Lake Hayes exhibit a facultative phototropism with a negative reaction to direct sunlight but a positive reaction to weak light.

I. INTRODUCTION

Both the North and the South Islands of New Zealand contain many lakes, the altitudinal range, depth, and location of which provide a great variety of conditions. A number of these lakes with their tributary streams offer some of the finest trout fishing in the world.

Few contributions have been made to a limnological study of any of these lakes. Armstrong (1935) studied the general ecology of Lake Taupo, and Flint (1938) surveyed the phytoplankton of Lake Sarah. An unpublished report by Professor E. Percival of Canterbury University College records briefly the results of tow nettings made in 37 South Island lakes.

The aim of this investigation is to make a preliminary survey of the macroplankton of Lake Hayes and of such factors as contribute to its general productivity.

Lake Hayes was chosen, after preliminary samplings had been made in Lakes Taupo, Rotorua, Tarawera, Te Anau, and Wakatipu, for the following reasons:

(1) A dense plankton in comparison with other lakes.

(2) A depth sufficient to permit observation of diurnal migration, in association with an area sufficiently small to allow coverage by a single operator.

(3) Location in an area reasonably accessible (170 miles from Dunedin) and relatively unpopulated.

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The lake is a game sanctuary but is open to trout fishing from November to April. Eight visits, covering a variety of conditions, were made over a period of two years and two months.

II. The Lake

(*a*) *Morphology*

Lake Hayes lies in the South Island of New Zealand, latitude 44°59′ S., longitude 168°48′ E. It is a freshwater lake, 1,080 ft. above sea-level and 655 acres in area. Its greatest length is just under 2 miles while its width varies from 30 to 50 ch. The shape is roughly that of a parallelogram with its long axis in a NNE. to SSW. direction (Fig. 1). East and west the shores are bounded by rocky cliffs above which rise smoothed and undulating terraces. The north end is bordered by a somewhat swampy flat beyond which is a terrace formed of moraine gravels and silt. The southern end is also swampy and gives rise to an alluvial terrace formed of silt and calcareous ooze (Plate 1, Fig. 2).

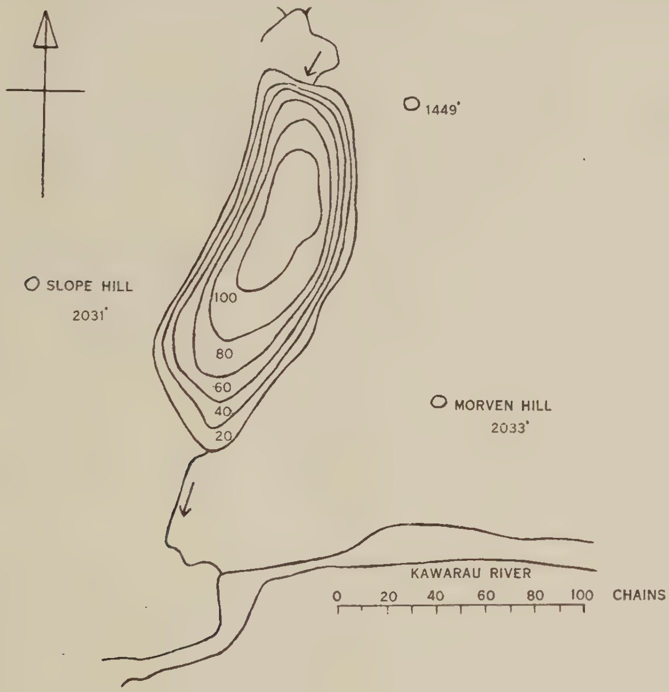


Fig. 1.—Contour map of Lake Hayes. Contour interval, 20 ft. (From N.Z. Geological Survey, Bulletin No. 7, 1909.)

The greatest depth is 108 ft. (18 fathoms); for over a mile in length the depth exceeds 100 ft. (approx. 17 fathoms) and for over two-thirds of the area it exceeds 60 ft. (10 fathoms). The water deepens rapidly on the east and west sides, more gradually at the north end, while the gradient is low at the southern or outlet end (see Fig. 1).

(*b*) *History*

Park (1909) considers that the Lake Wakatipu region was covered, during the Pleistocene glaciation, by an immense ice sheet many thousands of feet thick. This was succeeded by 'Glacial Lake Wakatipu' with a level 150 ft. above that of the present lake and covering a large area, including the present Lake Hayes and the surrounding flat country.

Lake Hayes lies in a rocky basin dammed by glacial terraces (Plate 1, Fig. 3). However, a fault crosses the east side of the lake and Park says, "It is a matter of conjecture to what extent the basin is due to faulting, but that the Soho fault formed a line of dislocation which offered favourable conditions for the operation of fluviatile and glacier erosion is a conclusion that seems to be warranted by the existing circumstances".

(*c*) *Drainage*

The main inlet enters midway along the northern shore (Plate 1, Fig. 3). This stream is approximately 4 miles long, rises amongst moraine terraces, and runs through rough grazing country. Therefore the lake is not normally snow fed. A small creek arising from a spring, close to the edge, enters in the north-west corner. Slight seasonal seepage enters from springs on the eastern and western sides. The outlet occurs in a raupo swamp on the eastern side of the south end (Fig. 1). It is very slow-moving and, after less than a mile joins the Kawarau River.

It is unlikely that there is any through drainage in the lake. The temperature of the main inlet (12°C. on 27.ii.49), and the spring-fed inlet (13°C.) is less than the upper surface temperature of the lake (15.5°C.) so that the denser incoming water sinks into the lake basin.

(*d*) *Vegetation*

There is no natural forest near the shore-line, and the surrounding country indicates that scrubby vegetation has been characteristic since the formation of the modern lake. Willows (*Salix babylonica* and some *S. fragilis*), line the northern end (Plate 1, Fig. 1). Other small groups are dotted along the shores of the east and south, with one group on the west. There are also a few lombardy poplars and a small plantation of eucalypts on the eastern shore. The cliffs are sparsely covered with a mixture of indigenous and exotic shrubs. In a few favourable places grasses reach the edge of the water.

Since the eastern and western littoral zones are formed of slabs of schist and the northern is a gravel beach, there is singularly little emergent vegetation. The only significant area is at the southern end and consists of raupo—*Typha muelleri* Rohrb.—swamp. In one shallow bay there is a small amount of *Myriophyllum* and *Potamogeton*.

Azolla rubra (R.Br.) is frequently found floating in the lake, swept there by the wind from dense patches located in the shallows at the southern end.

The commonest attached alga, *Ulothrix* sp., is found growing on the rock slabs and willow roots.

(*e*) *Climate*

The data below were recorded at the Queenstown station, 8 miles from the southern end of Lake Hayes, and will approximate to the lake conditions.

Average annual maximum temperature 58.7°F.

Average annual minimum temperature 40.9°F.

Average annual number hours of bright sunshine 1,999.

Average annual rainfall (no seasonal maximum) 30.78 in.

Percentage of frequency of winds at 0930 hr.: N. 14; NE. 4; E. 2; SE. 6; S. 7; SW. 10; W. 9; NW. 19; calm 29. (These figures were supplied by the Meteorological Branch of the Air Department.) It will be noted that calm days were infrequent, a factor that often interfered with sampling conditions.

(*f*) *Physical Conditions*

(i) *Turbidity.*—Records were obtained by using a Secchi disc of white porcelain, 20 cm. in diameter. Readings (Table 1) were all made near midday.

TABLE 1

SECCHI DISC TURBIDITY READINGS

Date	Depth (m.)
27. iii.48	4.6
22. ii.49	3.9
15. iv.49	3.6
8. vii.49	4.0
27.viii.49	3.1
4. ii.50	4.0
16. v.50	4.5

Variation, as shown by the figures, is not great, the period of greatest turbidity occurring in spring at the peak of phytoplankton production (Fig. 5).

By comparison, Lake Wakatipu, 8 miles away, showed a Secchi disc reading of 8.1 m. on March 28, 1948. The considerably decreased turbidity may be due to a paucity of plankton in Lake Wakatipu related to its great depth (approx. 1,200 ft.).

(ii) *Thermal Conditions.*—During February 1949, temperature readings at depth were made by lowering a thermometer in an empty, corked bottle from which the cork was removed at the required depth and which, after 5 min. immersion, was hauled rapidly to the surface and the thermometer read. These readings indicated the likelihood of a thermocline but the method was not considered sufficiently accurate and was abandoned.

Since a reversing thermometer was not available, subsequent readings were made with a maximum and minimum thermometer, weighted and lowered by a marked cotton cord. The surface temperatures never fell below 4°C., and numerous records taken from various regions at the lake showed no temperature abnormalities. Therefore it is considered that the data obtained by the above means are reliable. The thermometer was calibrated before and after use, and was accurate to 0.25°C.

The cotton cord was tested and showed a slight variation due to shrinkage when wet, but since the figures quoted (Table 2) are relative, no corrections have been attempted.

TABLE 2

SEASONAL AND VERTICAL VARIATIONS OF WATER TEMPERATURE (°C.)

Depth (fathoms)	27.ii.49	18.iv.49	8.vii.49	25.viii.49	22.xi.49	4.ii.50	15.v.50
0	15.5	12.2	6.6	5.8	14.4	17.7	11.0
1	15.0	12.2	6.6	5.5	14.4	17.7	11.0
2	14.8	12.0	6.6	5.5	14.4	17.5	10.5
3	14.8	11.6	6.6	5.5	14.4	17.2	10.5
4	14.4	11.6	6.3	5.5	14.4	17.0	10.2
5	14.4	11.6	6.3	5.5	14.0	16.1	10.2
6	13.8	11.6	6.1	5.5	13.8	15.0	10.2
7	13.3	11.6	6.1	5.5	12.2	12.2	10.2
8	12.7	11.6	6.1	5.5	10.0	10.0	10.2
9	11.1	11.6	6.1	5.5	9.4	9.4	10.2
10	10.0	11.1	6.0	5.5	9.0	8.8	10.2
11	8.8	11.1	6.0	5.5	7.7	8.6	10.2
12	8.8	10.5	6.0	5.5	7.5	8.3	10.2
13	8.8	10.0	5.5	5.5	7.5	8.3	10.2
14	8.4	9.4	5.5	5.5	7.2	8.3	10.0
15	8.0	8.8	5.5	5.5	7.2	8.3	7.7
16	7.7	8.8	5.5	5.5	7.2	7.7	7.7
17	7.7	8.8	5.5	5.5	7.0	7.7	7.7
18	7.7	8.8	5.5	5.5	6.6	7.7	7.7

The figures quoted in Table 2 indicate that a thermal stratification (Fig. 2) occurs in Lake Hayes during the late spring, summer, and autumn months with a complete overturn during the late winter.

The lake would seem to be a Tropical Lake, Order 2, as detailed by Welch (1935), i.e. surface temperatures always above 4°C.; temperature of bottom water varies, but not far from 4°C.; one circulation period in winter.

III. PLANKTON

(*a*) *Methods of Sampling*

The net was of the usual Nansen pattern, 65 cm. long, with an opening 30 cm. in diameter. It was made of 6X bolting silk, i.e. 74 meshes to the sq. in., with a 10 cm. entrance of japara cloth. The latter carried the rings used for throttling the net during vertical hauls. Instead of the usual bucket attachment, a 4 oz. jar was tied to the open end and the sample was preserved without transference to another container. If the haul was particularly heavy the net was washed off into a second jar.

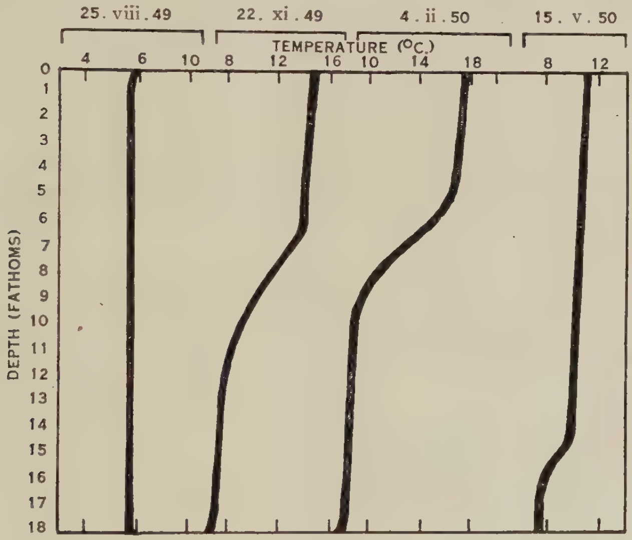


Fig. 2.—Vertical and seasonal ranges of temperature in Lake Hayes.

All tows, close to the surface, were made by a line extending 2 fathoms beyond the stern of the boat. Unless otherwise stated, all were of 15 min. duration over water not less than 10 fathoms deep. The same courses were towed on fixed landmarks, rowing 5 min. in a direct line, 5 min. turning in a wide arc, and then 5 min. retracing the outward course. It was hoped this would reduce the variations due to wind and waves.

Diurnal samples were taken two-hourly over a 24-hour period. For night sampling an attempt to fix the starting point was made by counting the strokes out from shore. A flashlight was used only to ascertain the towing position of the net in order that there should be a minimum of interference with natural lighting.

Precautions were taken to maintain a constant towing speed but variations at night, particularly during windy and rough weather, may have occurred.

(*b*) *Methods of Analysis of Samples*

The fixed samples were analysed and counted after return to the laboratory. The whole sample was mixed and 5 ml. were drawn off by a syringe. This aliquot was diluted to 100 ml. and five samples of 5 ml. were counted in a counting cell. From the average of the five samples the total numbers of each sample were computed.

A detailed analysis of the zooplankton only was attempted. A rough estimate was made of those components of the phytoplankton that were taken in abundance. This was obtained by taking a drop from a typical sample and counting the numbers per drop. Five drops were counted and the average figure taken as an estimate of variability in occurrence. The coarse net used for the zooplankton collected only the larger species of phytoplankton.

(*c*) *Systematic Description of the Plankton*

Phylum Coelenterata:

Hydra viridis, a facultative plankter, was taken in very small numbers in the net in April 1949.

Phylum Rotifera:

- *Asplanchnopus multiceps* (Schrank)
- *Pedalia mira* (Hudson)
- *Keratella quadrata* (Müller)
- *Keratella* sp.
- *Synchaeta oblongata* (Ehrenberg)
- *S. pactinata* (Ehrenberg)
- *Polyarthra trigla* (Ehrenberg)

Phylum Arthropoda:

- Arachnida:
  - Hydracarina
- Crustacea:
  - Copepoda: Genus *Boeckella* (*Boeckia,* Thomson, 1883) (*Boeckella,* de Guerne, and Richard, 1889)
    - Genus *Cyclops*
  - Cladocera:
    - Family Daphniidae:
      - Genus *Daphnia*
      - Genus *Ceriodaphnia*
    - Family Bosminidae:
      - Genus *Bosmina*

Most of the zooplankton is composed of copepods and cladocera. *Cyclops* never appeared prominently, and was less than the ratio 1 in 100 in comparison with *Boeckella.*

Rotifers and hydracarina appeared in small numbers in most nettings.

Chironomid larvae and ostracods were noted in bottom deposits. Insect larvae were rarely present in any surface tows.

A comprehensive survey of the phytoplankton was not attempted but its dominant constituents are as follows:

Myxophyceae	Nostocaceae	*Anabaena* sp.
Bacillariales	Centricae	Melosiraceae. *Melosira* sp.
Dinophyceae	Peridinaceae	*Peridinium* sp.
Chlorococcales	Selenastraceae	*Closteriopsis* sp.
Volvocales	Sphaerellaceae	*Volvox* sp.
Conjugatae	Desmidiaceae	*Staurastrum* sp.

(*d*) *Seasonal Fluctuations of the Plankton*

A series of graphs and diagrams have been drawn up to illustrate diurnal and seasonal fluctuations of the significant organisms making up the plankton.

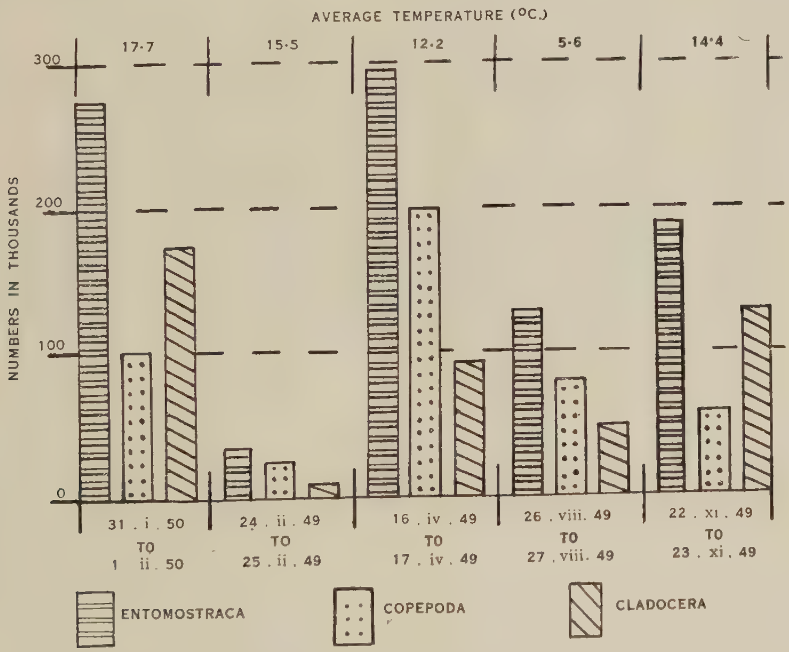


Fig. 3.—Seasonal variations of numbers of Entomostraca based on average figures of two-hourly diurnal samples.

Figure 3 indicates that seasonal variations occur quantitatively in the zooplankton of Lake Hayes. Peaks occur in summer and autumn, with the summer peak dominated by the cladocera and the autumn peak by the copepods. It is possible that a spring peak may have occurred during the interval between August 27 and November 11, 1949.

There would appear to be no relationship between temperature and productivity, for the temperatures are alike in February and November 1949 but the quantities differ.

Of the three genera of cladocera found in the lake, *Ceriodaphnia* is numerically the most important (Fig. 4). *Bosmina* never shows dominance and in only one instance does *Daphnia* exceed *Ceriodaphnia* in any significant amount. *Ceriodaphnia* would appear to achieve its maximum in a higher temperature than does *Daphnia* but variations are doubtless due to a combination of factors.

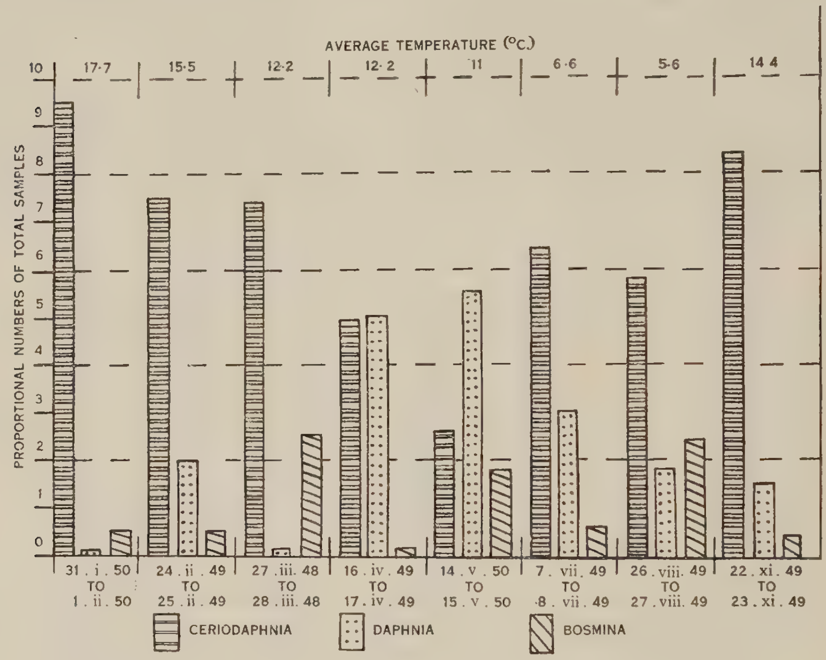


Fig. 4.—Seasonal proportional relationships between three genera of cladocera, based on average figures of two-hourly diurnal samples.

The relative sizes of these animals throw a different light on their importance in the plankton. Sizes quoted are the average of 25 samples of egg-bearing females:

Daphnia, length (exclusive of spine) 2.38 mm., depth 1.25 mm.;
Ceriodaphnia, length (exclusive of spine) 0.7 mm., depth 0.5 mm.;
Bosmina, length (exclusive of spine) 0.34 mm.; depth 0.275 mm.

If, from the above measurements, we picture the third dimension, relative in proportion, it will be seen that numbers alone do not give a true picture of the food value of the constituents of the macroplankton. *Daphnia* show a greater value than their numbers imply while *Bosmina* dwindle in importance.

In Figure 5 the principal constituents of the plankton are rated on an eight point scale to show the relationship between the zooplankton and the phytoplankton.

Melosira and *Closteriopsis* are the outstanding algae of the phytoplankton. Each, during its maximum, gives an outstanding character to the water. The diatom *Melosira,* in conjunction with the desmid *Staurastrum,* confers a green, translucent coloration, while *Closteriopsis* gives a more golden appearance, glinting as the sun shines on to it.

The maxima of the zooplankton and phytoplankton do not coincide. Little correlation appears to exist although *Daphnia* appears more frequently with *Melosira* and *Ceriodaphnia* with *Closteriopsis.*

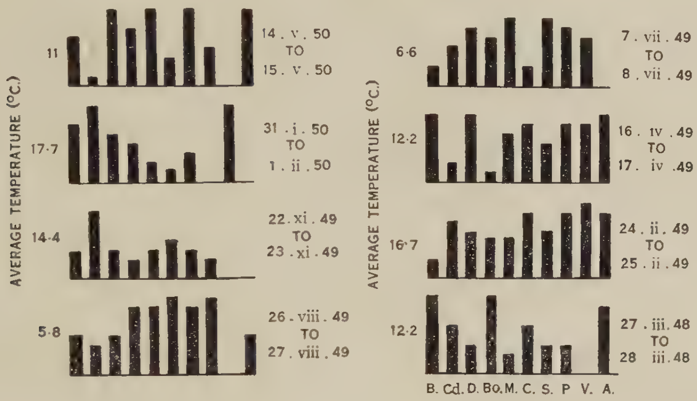


Fig. 5.—Seasonal gradation from maximum to minimum range of phytoplankton and zooplankton genera. Diagram based on eight point scale. *B., Boeckella; Cd., Ceriodaphnia; D., Daphnia; Bo., Bosmina; M., Melosira; C., Closteriopsis; S., Staurastrum; P., Peridinium; V., Volvox; A. Anabaena.*

(*e*) *Vertical Distribution*

Vertical hauls with a closing net (Table 3) show that the greatest number of animals were located in the upper 6 fathoms, i.e. in the epilimnion (Fig. 2). However, small quantities are found below the thermocline. No qualitative differences occurred in the varying strata.

From the present investigation it is not possible to say whether migrations took place through the whole vertical range or if particular populations showed facultative preference for the stratum below the thermocline. *Cyclops* shows a preference for deeper waters but not for the bottom depths.

(*f*) *Diurnal Migrations of the Zooplankton*

Table 4 sets out the physical conditions that prevailed during the hours at which diurnal samples were made. Wind force was estimated according to the Beaufort Scale. Conditions of light are indicated by the variation from starlight to sunlight. Since high cliffs and hills skirt the eastern and western shores, the rays of the sun do not reach the water until approximately one hour after the sun has risen and are lost one hour before its actual setting. "Sun up" therefore means sun on the water, while dawn and dusk indicate the protracted periods when there was light but no direct sunshine. The table indicates whether the sky was clear, overcast, or partially covered by scattered clouds.

TABLE 3

VERTICAL DISTRIBUTION OF ENTOMOSTRACA

Date		Depth (fathoms)		
		6-Surface	12-6	18-12
22. ii.49	*Bk.*	2,116	424	490
	Cy.	—	105	82
	Cd.	354	176	95
	D.	14	—	5
	Bos.	—	6	—
18. iv.49	*Bk.*	5,828	478	99
	Cy.	6	26	9
	Cd.	2,022	128	86
	D.	26	—	2
	Bos.	40	26	4
30.viii.49	*Bk.*	2,166	289	283
	Cy.	—	—	1
	Cd.	198	68	6
	D.	58	9	34
	Bos.	66	17	17
1. ii.50	*Bk.*	5,597	2,995	1,248
	Cy.	—	—	—
	Cd.	7,235	5,748	1,245
	D.	23	29	14
	Bos.	471	234	109

Bk. = *Boeckella*, *Cy.* = *Cyclops*, *Cd.* = *Ceriodaphnia*, *D.* = *Daphnia*, *Bos.* = *Bosmina.*

TABLE 4

PHYSICAL CONDITIONS DURING DIURNAL SAMPLING PERIODS

Date	Hours	Water Temp. (°C.)	Wind	Light	Sky
24. ii.49 to	0	15.6	1	Starlight	Clear
25. ii.49	2	15.0	1	Starlight	Clear
	4	15.0	1	Weak moon	Clear
	6	15.0	2	Dawn	Clear
	8	15.0	4	Sun up	Overcast
	10	15.6	0	Sun up	Overcast
	12	16.7	0	Sun up	Some cloud
	14	17.2	2	Sun up	Some cloud
	16	16.7	5	Sun up	Some cloud
	18	15.6	2	Dusk	Some cloud
	20	15.6	1	Starlight	Clear
	22	15.6	1	Starlight	Clear

TABLE 4 (*Continued*)

Date	Hours	Water Temp. (°C.)	Wind	Light	Sky
16. iv.49 to 17. iv.49	1	11.7	0	Moonlight	Clear
	3	11.7	0	Moonlight	Clear
	5	11.7	1	Moonlight	Some cloud
	7	11.7	1	Dawn	Some cloud
	9	11.7	2	Sun up	Overcast
	11	11.7	1	Sun up	Overcast
	13	11.9	2	Sun up	Overcast
	15	12.0	3	Sun up	Overcast
	17	12.0	2	Dusk	Overcast
	19	11.9	2	Moonlight	Clear
	21	11.7	2	Moonlight	Clear
	23	11.7	2	Moonlight	Clear
26.viii.49 to 27.viii.49	0	5.0	0	Starlight	Clear
	2	5.0	0	Starlight	Clear
	4	5.0	0	Starlight	Some cloud
	6	5.0	½	Dawn	Some cloud
	8	5.4	0	Sun up	Overcast
	10	5.6	0	Sun up	Overcast
	12	5.8	0	Sun up	Some cloud
	14	5.8	2	Sun up	Some cloud
	16	5.8	1	Sun up	Some cloud
	18	5.8	0	Dusk	Some cloud
26.viii.49 to 27.viii.49	20	5.8	1	Starlight	Some cloud
	22	5.6	0	Starlight	Clear
22. xi.49 to 23. xi.49	1	15.7	0	Starlight	Clear
	3	15.7	0	Starlight	Clear
	5	15.5	0	Dawn	Clear
	7	15.5	0	Sun up	Clear
	9	15.5	0	Sun up	Clear
	11	16.0	0	Sun up	Clear
	13	16.5	3	Sun up	Some cloud
	15	16.8	5	Sun up	Overcast
	17	17.0	4	Sun up	Overcast
	19	16.0	1	Sun up	Clear
	21	15.7	1	Dusk	Clear
	23	15.7	1	Starlight	Clear
31. i.50 to 1. ii.50	0	18.0	½	Moonlight	Clear
	2	18.0	1	Starlight	Clear
	4	18.0	2	Starlight	Clear
	6	18.0	1	Dawn	Clear
	8	18.0	1	Sun up	Clear
	10	18.5	2	Sun up	Clear
	12	19.2	½	Sun up	Clear
	14	19.5	2	Sun up	Clear
	16	19.5	3	Sun up	Clear
	18	19.5	3	Sun up	Clear
	20	18.5	4	Dusk	Clear
	22	18.0	1	Moonlight	Clear

Figure 6, in conjunction with Table 4, illustrates the numbers of Entomostraca congregated in the surface waters at definite times under certain conditions. It will be noted that there is a migratory behaviour conforming to a general rhythm exhibited by both the copepods and cladocera in which "lows" occur in the vicinity of midday or when the sun is nearly vertical. No compensatory maxima are shown during the hours of darkness but peak periods, in general, appear at dawn and at dusk when the sun is off the water but when there is some light. The only significant peaks that occur during the hours the sun is up are on February 24, 1949 and April 16, 1949. Table 4 shows that during the day of April 16 the sky was overcast and a wind was blowing. On February 24 the peak at 16.00 hours occurs with conditions of some cloud and strong wind.

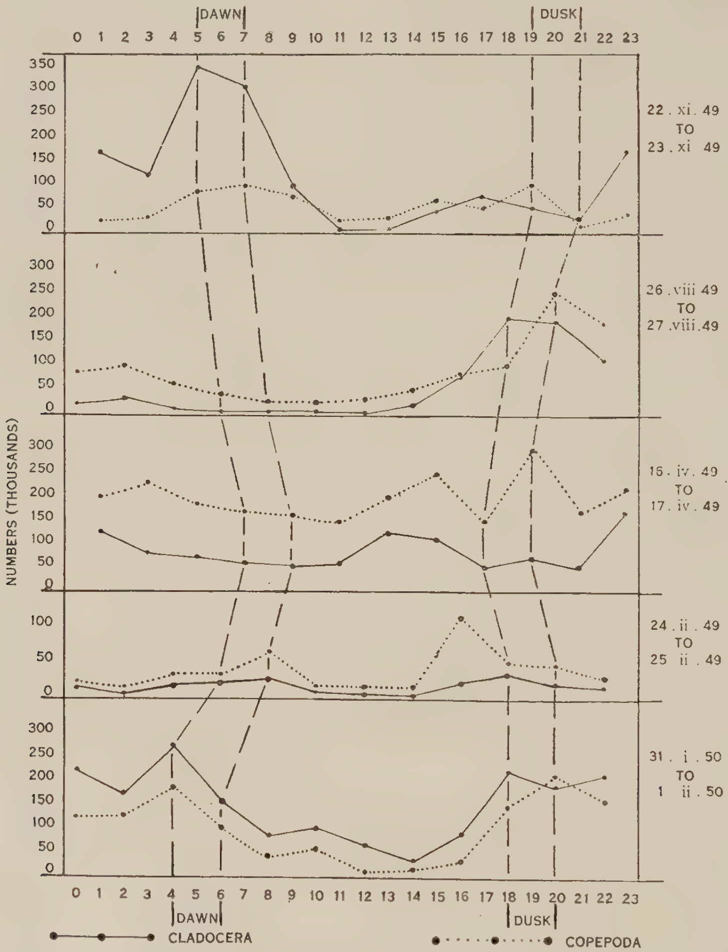


Fig. 6.—Seasonal and diurnal migrations of copepods and cladocera, based on two-hourly diurnal samples. ●——● Cladocera; ●. . . .● Copepoda.

The wind introduces two factors which may interfere with normal behaviour, firstly, unequal horizontal distribution due to the creation of

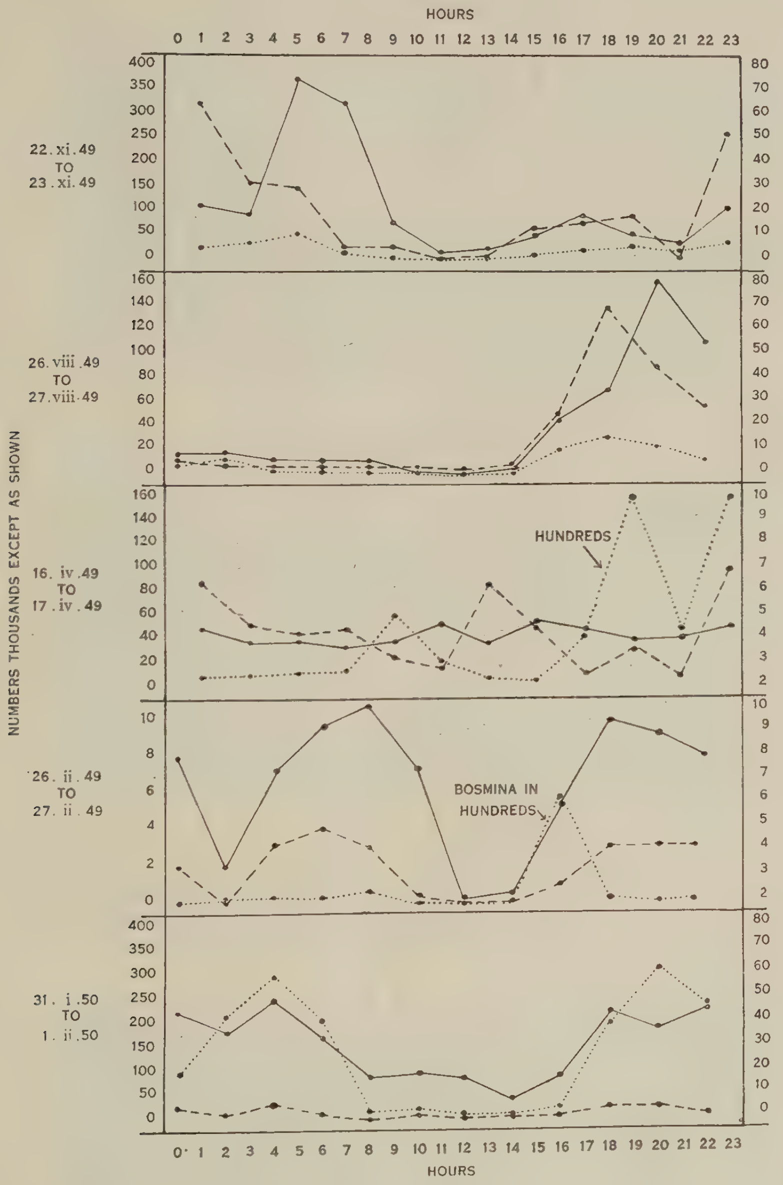


Fig. 7.—Seasonal and diurnal migrations of the three genera of cladocera, based on two-hourly diurnal samples. ●——● *Ceriodaphnia;* ● - - - - ● *Daphnia;* ● . . . . ● *Bosmina.*

surface currents directed towards the exposed shore and secondly, interference with the angle at which the light penetrates the water caused by wave action.

No correlation is shown between temperature changes and the convection currents they may initiate since, though the "lows" occur during the periods of high temperature, peaks occur during both high and low temperatures.

Figure 7 demonstrates that the genera of cladocera all maintain a rhythm similar to that exhibited by the total numbers of cladocera as plotted against the copepods in Figure 6.

Figures 6 and 7, considered with Table 4, indicate that though a combination of factors may interact to cause the migratory behaviour of the entomostracan fauna of Lake Hayes, a facultative phototropism exists with a negative reaction to direct sunlight and a positive reaction to weak light.

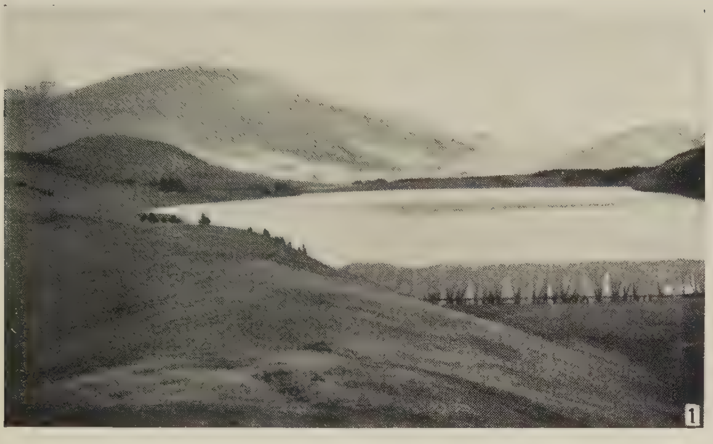
IV. Discussion

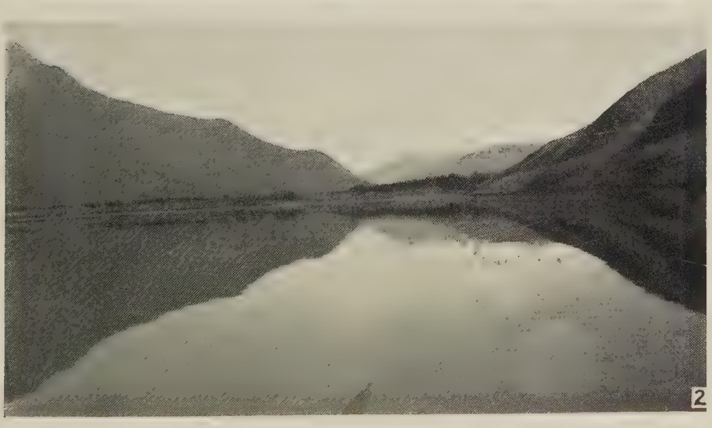
Of the five genera of Entomostraca represented in the plankton of Lake Hayes, four, *Cyclops, Daphnia, Ceriodaphnia,* and *Bosmina* are widely distributed. The literature references to these genera are too numerous to be individually mentioned but species are noted from such varied localities as Erh Hai, China (Hsiao 1949), Africa (Cunnington 1920), Ireland (Southern and Gardiner 1926), North America (Ward and Whipple 1918). The fifth genus, *Boeckella,* occurs only in the southern hemisphere except for one species, *B. orientalis,* recorded from Mongolia, and which Marsh (1924) considers may have been given an incorrect location. Sars (1894) notes that *B. triarticulata,* the species from which the genus was originally described, closely resembles the northern hemisphere genus *Diaptomus* in habits and appearance. It is considered that the above five genera are represented by five species only but their systematic position is left for discussion in a later paper.

Brady (1906) and Henry (1924) note that few species of Entomostraca occur in New Zealand lakes. In comparison with lakes such as Mendota—12 species (Birge 1897), Nipissing—12 (Langford 1938), Lucerne—9 (Worthington 1931), Lough Derg—67 (Southern and Gardiner 1926), Lake Hayes shows a characteristic lack of diversity in its macroplankton.

Many observations have been recorded on the diurnal movements of zooplankton and many hypotheses contributed on the causes which inaugurate these migrations (see Russell 1927). The vertical movements of the animals have been calculated from the numbers collected in samples taken at different levels, either by a horizontally towed net (Russell 1934), a vertically hauled closing net (Worthington 1931), or a plankton trap (Langford 1938). Recent work on Lake Maggiore by Baldi, Cavalli, and Pirocchi (1947) and Tonolli (1949) has shown that sampling by the horizontal method is preferable for any research based on quantitative analysis.

Russell (1927) discusses the factors controlling the vertical distribution of plankton. He says, "that light is evidently a factor of great





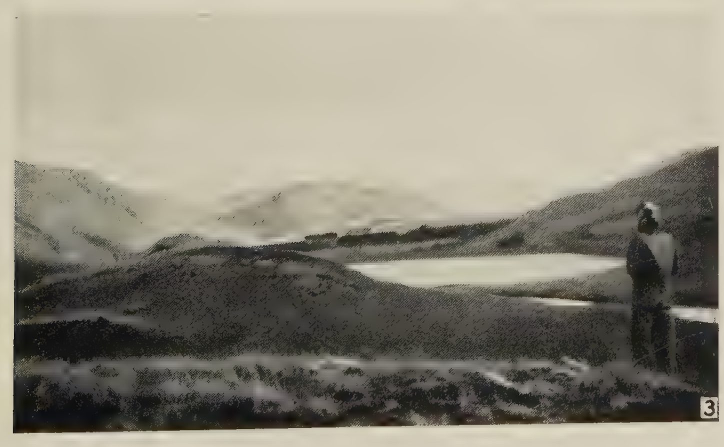


Fig. 1.—Lake Hayes under winter conditions. View taken facing south-east. Northern shore fringed with willows in foreground and southern shore in the distance.

Fig. 2.—Lake Hayes. View of southern shore taken from the lake in winter.

Fig. 3.—Lake Hayes viewed from the south-east. Inlet shown in right foreground.

importance seems to be in common agreement; but we have seen that there has been considerable difference in opinion as to how it acts". The recognition of light as a controlling factor in migration and the development of improved methods for measuring light (Atkins and Paul 1933) led to a fresh line of attack on the problem of migration. Measurements of light intensity, both surface and subsurface, were correlated with the movements of the macroplankton. Such investigations have been described by Russell (1934), Clarke (1933, 1934), Ullyott (1939), Johnson and Raymont (1939), and Spooner (1934). The conclusions reached vary but, as Clarke (1936) says, "if there is one generality which can safely be made about the migration of plankton, it is that the phenomenon is an extremely variable one. Not only do different species behave differently but the reaction of the same species may be quite contrary in one locality to what it is in another, or in the same locality at different times". Clarke finds the variation in intensity of daylight during a 24-hour period the most important factor controlling migration but considers that the reactions of the various plankton organisms to light are easily modified by slight changes in their environment or physiological state.

Welch (1935) enumerates the various theories proposed to account for diurnal movements of the plankton. Worthington's (1931) hypothesis of an interaction between a negative geotropism and a negative heliotropism is supported by Ullyott (1939) who correlates the diurnal migrations of *Cyclops strenuus* in Lake Windermere with variations in light intensity. It is also supported by Clarke (1936), who suggests that negative geotropism is less effective in the afternoon when an adaptation to light has taken place, and that if a withdrawal from the surface takes place before dawn we must assume another factor that causes a reverse geotropism.

Observations on the diurnal movements of the Entomostraca of Lake Hayes are recorded for two reasons. Firstly, previous records have been made chiefly from summer and not from seasonal sampling. Secondly, no such observations have been previously recorded for the Australasian region. Since the horizontal tows were made in the surface waters only, no knowledge has been obtained of the depths to which the animals migrated when they were not in the upper layer.

Both the copepods and cladocera show a similar pattern of vertical migration. The peaks occurring in the vicinity of dawn and dusk show a congregation in the surface waters at a period of low light intensity, while the lows that occur at midday indicate an aversion to strong light. An abundance but no optimum is maintained during the hours of darkness (Fig. 6).

These movements have no direct relationship with temperature for, while the lows, in general, occur during periods of maximum temperature, the peaks occur with both high and low temperatures. Food supply is probably a factor that adds desirability to the upper waters but can be secondary only since it is not sufficiently strong to hold the organisms there against the repelling influence of strong light. Therefore, from the present study, it appears that light intensity is the most important factor governing vertical distribution. If Figure 6 is studied in conjunction with Table 4 it will be seen that, while a negative phototropism is exhibited towards strong light, a facultative phototropism is exhibited towards certain lights and the normal pattern is upset by a crowding in the upper water during times when the sky is overcast and the water rough (e.g. afternoon sampling period for February 24, 1949). This optimum light preference has been noted by Russell (1927). When the optimum light no longer prevails there is probably a dispersal to regions that offer the greatest food supply.

The Entomostraca of Lake Hayes would appear therefore to conform to the general pattern of behaviour exhibited by most planktonic species, that is they move from the surface waters during the periods of strong light and towards the surface when it is no longer strongly illuminated. They differ somewhat from the behaviour usually recorded in that they do not remain thickly congregated in the upper strata all night but show an upward movement at dawn.

Further conclusions may be drawn from more extensive investigations, which should include horizontal tows at regular depths with a Clarke and Bumpus plankton sampler (Clarke and Bumpus 1940) and the measurement of surface and subsurface illumination. The sampling should be made from more than one station and should be continued at regular intervals for at least a season. The different age-groups and sexes (where possible) of each species should be counted.

V. ACKNOWLEDGMENTS

My thanks are due to Professor B. J. Marples and members of the Zoology Department, University of Otago, for their assistance and encouragement in making this study; to Mr. D. F. Hobbs of the Marine Department; to the Department of Internal Affairs for general assistance and for facilitating transport; and to Mr. P. Parr, University of Otago, for the identification of rotifers.

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AN APPLICATION OF VISIBLE INDEXING TO SYSTEMATIC ZOOLOGY

By I. S. R. MUNRO*

(*Manuscript received September* 21, 1951)

Summary

A method of cataloguing and cross-indexing taxonomic, nomenclatural, and distributional data has been developed as a model technique in filing for biologists specializing in systematics. The technique was developed expressly for the compilation of a laboratory guide to the fish fauna of Australia. The system employs standard modern equipment, combining horizontal visible filing in trays for the main catalogue and rotary-mounted card units for cross-indexing. The units of equipment, design of cards, arrangement of units, arrangement of data, and scope of material are described in detail. Reasons are given for the selection of equipment and for the methods adopted. Manipulation of the index and its component parts is explained.

I. INTRODUCTION

The Division of Fisheries, Commonwealth Scientific and Industrial Research Organization, has recently compiled a comprehensive reference catalogue of the fish fauna of Australia, New Guinea, and Lord Howe Island. This was designed as a complete basic reference for the ichthyological investigations in the area. It replaces and supplements existing checklists. The system employs modern visible-filing techniques and utilizes standard equipment. The method is a departure from that usually adopted by systematists and may have wider application amongst such workers.

II. FILING EQUIPMENT

The reference system consists of two parts comprising a species catalogue and a cross-index. The catalogue is essentially a collection of unit records representing individual species, which are arranged in systematic order, and filed according to families and genera. Flat filing is used for this purpose, and records are housed in standard-pattern, steel, visible-filing cabinets, which contain tiers of horizontal trays equipped with interchangeable pockets. Pockets measuring 8 by 5 in. are a convenient size. The types of cards, inserts, and signals are illustrated in Figure 1. The cabinets measure approximately 12 in. wide and 24 in. deep. The cross-index is employed to locate specific, generic, family, and common names, and titles of ichthyological articles. These records are filed alphabetically on $2\frac{1}{2} \times 4$ in. cards mounted on rotating wheels instead of in drawers.

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III. SPECIES CATALOGUE

(a) *Family Cards*

Species are grouped in sections which represent families. The leading pocket in each such section carries data relevant only to that family, including family characters, key to genera, and references to generic descriptions and genotypes. Cards are unruled and data are typewritten. Family pockets are distinguished by white, visible margins which show a black signal on the left, family name in black capitals in the centre, and a number* in black on the right. Family name and number show also as a heading when the pocket is in the open position. In this position the number is indicated in red to afford contrast with the black numbers of the species cards. The numbering of pockets is part of the system of cross-indexing described below. Family numbers are also shown in the index windows on the front of each tray.

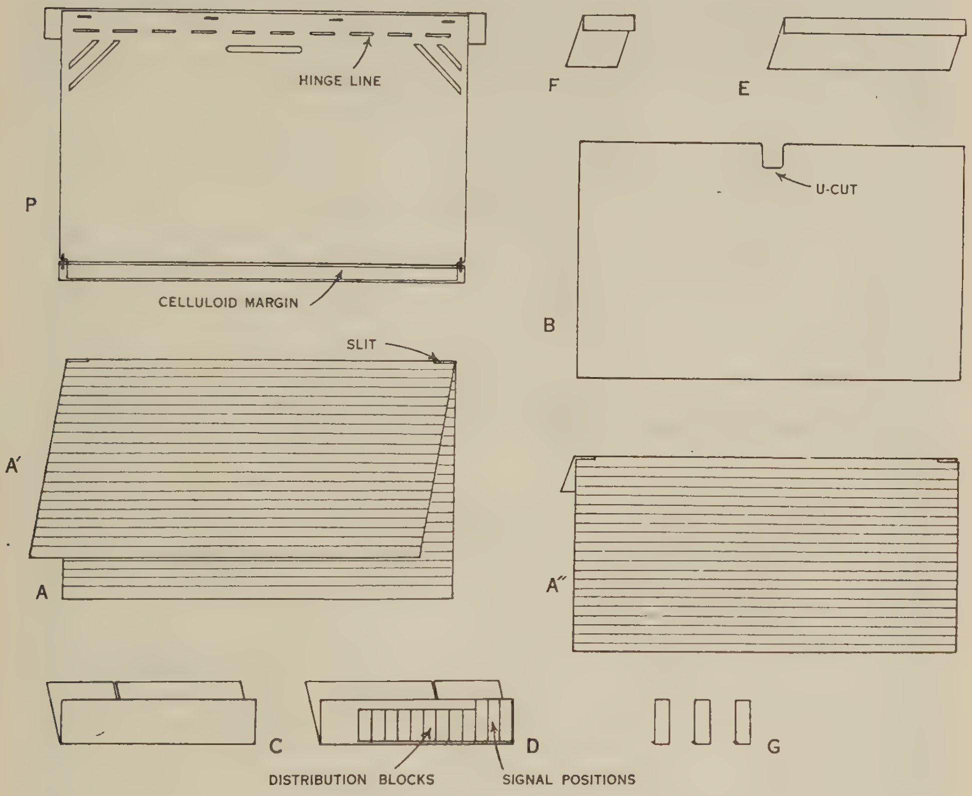

Fig. 1.—For explanation see text.

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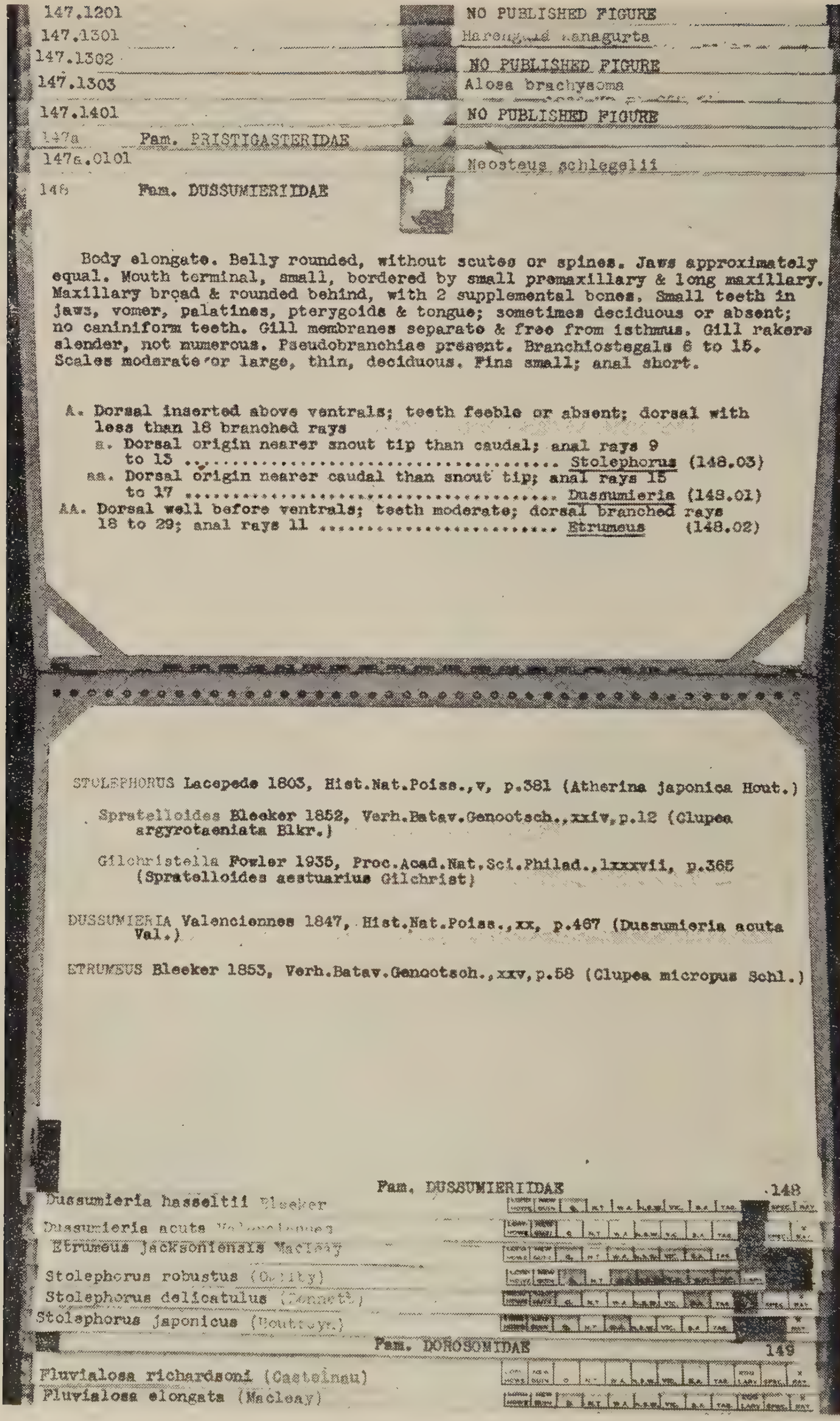
* Family number, based on Jordan (1923). –Stanford Univ. Publ. (Biol. Sci.), 111 (2); 79-243.



147.1201 NO PUBLISHED FIGURE
147.1301 Harengula kanagurta
147.1302 NO PUBLISHED FIGURE
147.1303 Alosa brachysoma
147.1401 NO PUBLISHED FIGURE
147a Fam. PRISTIGASTERIDAE
147a.0101 Neosteus schlegelii
148 Fam. DUSSUMIERIIDAE

Body elongate. Belly rounded, without scutes or spines. Jaws approximately equal. Mouth terminal, small, bordered by small premaxillary & long maxillary. Maxillary broad & rounded behind, with 2 supplemental bones. Small teeth in jaws, vomer, palatines, pterygoids & tongue; sometimes deciduous or absent; no caniniform teeth. Gill membranes separate & free from isthmus. Gill rakers slender, not numerous. Pseudobranchiae present. Branchiostegals 6 to 15. Scales moderate or large, thin, deciduous. Fins small; anal short.

A. Dorsal inserted above ventrals; teeth feeble or absent; dorsal with less than 18 branched rays
  a. Dorsal origin nearer snout tip than caudal; anal rays 9 to 13 .... Stolephorus (148.03)
  aa. Dorsal origin nearer caudal than snout tip; anal rays 15 to 17 .... Dussumieria (148.01)
AA. Dorsal well before ventrals; teeth moderate; dorsal branched rays 18 to 29; anal rays 11 .... Etrumeus (148.02)

STOLEPHORUS Lacepede 1803, Hist.Nat.Poiss.,v, p.381 (Atherina japonica Hout.)

Spratelloides Bleeker 1852, Verh.Batav.Genootsch.,xxiv,p.12 (Clupea argyrotaeniata Blkr.)

Gilchristella Fowler 1935, Proc.Acad.Nat.Sci.Philad.,lxxxvii, p.365 (Spratelloides aestuarius Gilchrist)

DUSSUMIERIA Valenciennes 1847, Hist.Nat.Poiss.,xx, p.467 (Dussumieria acuta Val.)

ETRUMEUS Bleeker 1853, Verh.Batav.Genootsch.,xxv,p.58 (Clupea micropus Schl.)

Fam. DUSSUMIERIIDAE 148
Dussumieria hasseltii Bleeker
Dussumieria acuta Valenciennes
Etrumeus jacksoniensis Macleay
Stolephorus robustus (Ogilby)
Stolephorus delicatulus (Bennett)
Stolephorus japonicus (Houttuyn)
Fam. DOROSOMIDAE 149
Fluvialosa richardsoni (Castelnau)
Fluvialosa elongata (Macleay)

Fig. 2.—Typical family record.

(b) *Orders and Suborders*

Provision is made for classification groupings higher than families, but special pockets are not allotted and their characters are not indicated. Ordinal, subordinal, and serial names show in the visible margins of the family cards. They occur only on the margin of the card belonging to the leading family in each higher grouping. Orders and suborders are emphasized by the presence of a red signal on the left, in addition to the normal black signal, which indicates a family pocket. Ordinal and subordinal names are in red upper case and red lower case respectively, and are placed to the left of the family name. Names of series are indicated in black upper case and are placed to the right of the family name. Ordinal names are repeated with subordinal names. Names of these higher groups are also shown in the index windows on the front of each tray.

(c) *Species Record*

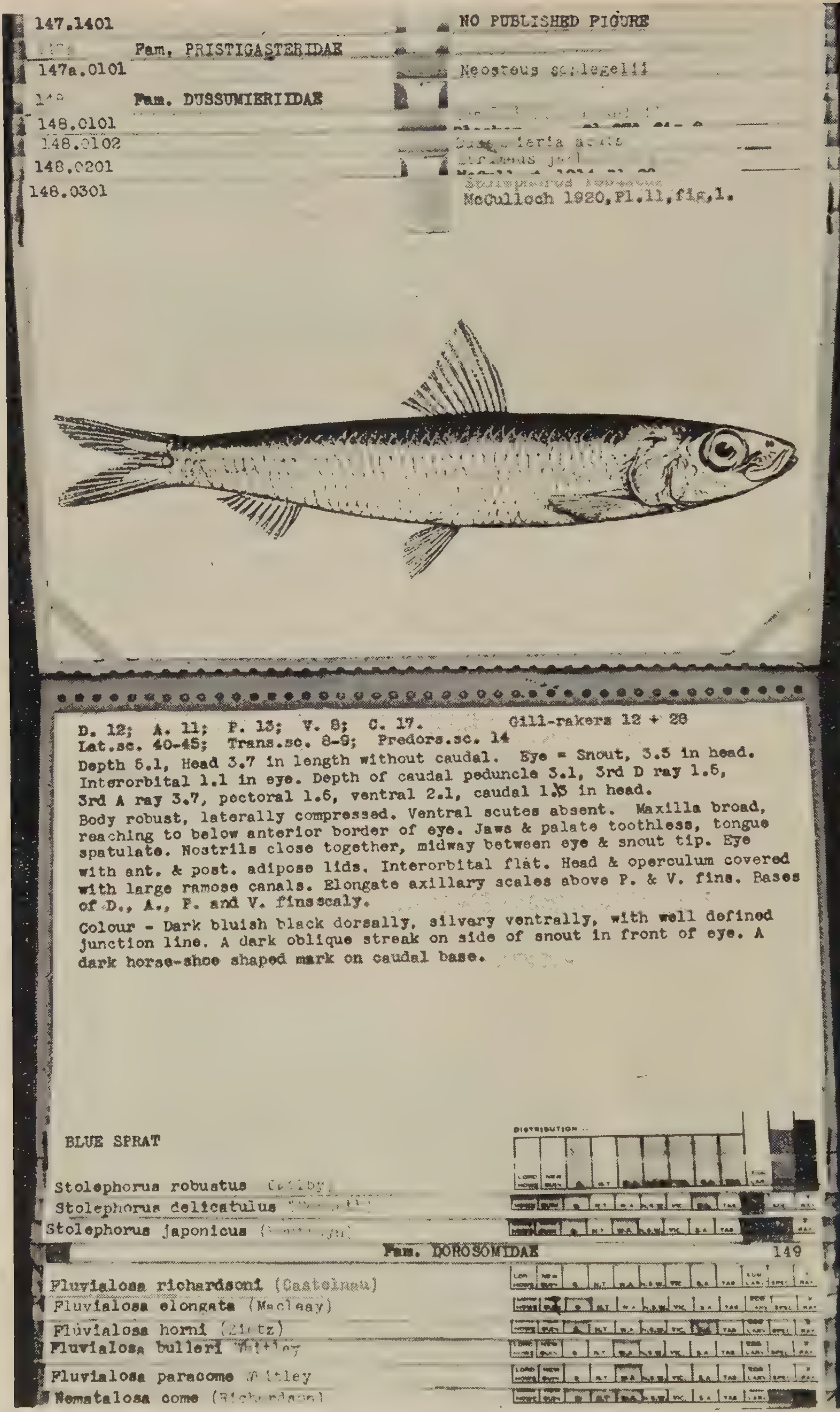
Several component cards and folded paper inserts are employed for each species record. These are illustrated in Figure 1. Components are interchangeable so that adjustments and alterations can be effected without defacing or interfering with the neatness of the unit as a whole. This is essential since changes in synonymy, nomenclature, and distribution frequently occur. The nature of the data included in the record, and the role played by component parts in the arrangement of these data, are as follows:

(i) *Scientific Name and Author.*—The scientific name, together with its author, shows in the visible margin on the left. Such names are arranged according to genera and do not follow alphabetic sequence in either genera or species. Generic and specific names are indicated in black and authors in red. Folded paper inserts (*C*) placed over the lower margins of the data cards (*A*;*A*′) avoid typing direct on the cards, and facilitate nomenclatural changes without re-writing the entire contents of the card.

(ii) *Common Name.*—This is not visible until the pocket is opened. It appears above the scientific name on the left marginal insert (*C*).

(iii) *Distribution.*—Distribution according to the political boundaries of the Australian states, New Guinea, and Lord Howe Island, also shows in the visible margins. A system of blocking is employed and a right marginal insert (*D*) has printed rectangles for each locality. These spaces are blocked in with red crayon-pencil according to indigenous distribution, or in blue for introduced species. Specific locality records are also included with the references listed on the inside of folded card (*A*,*A*′).

(iv) *Laboratory Reference.*—On the marginal insert (*D*) are three marked positions to the right of the distribution blocks. These are designed for the insertion of coloured celluloid signals (*G*) which show in the visible margin. In appropriate position, a green signal indicates that



147.1401 NO PUBLISHED FIGURE

Fam. PRISTIGASTERIDAE

147a.0101 Neosteus [illegible]legelii

Fam. DUSSUMIERIIDAE

148.0101

148.0102

148.0201

148.0301 McCulloch 1920, Pl. 11, fig. 1.

D. 12; A. 11; P. 13; V. 8; C. 17. Gill-rakers 12 + 28
Lat.sc. 40-45; Trans.sc. 8-9; Predors.sc. 14
Depth 5.1, Head 3.7 in length without caudal. Eye = Snout, 3.5 in head. Interorbital 1.1 in eye. Depth of caudal peduncle 3.1, 3rd D ray 1.6, 3rd A ray 3.7, pectoral 1.6, ventral 2.1, caudal 1.3 in head.
Body robust, laterally compressed. Ventral scutes absent. Maxilla broad, reaching to below anterior border of eye. Jaws & palate toothless, tongue spatulate. Nostrils close together, midway between eye & snout tip. Eye with ant. & post. adipose lids. Interorbital flat. Head & operculum covered with large ramose canals. Elongate axillary scales above P. & V. fins. Bases of D., A., P. and V. finsscaly.
Colour - Dark bluish black dorsally, silvery ventrally, with well defined junction line. A dark oblique streak on side of snout in front of eye. A dark horse-shoe shaped mark on caudal base.

BLUE SPRAT

DISTRIBUTION

Stolephorus robustus [illegible]
Stolephorus delicatulus [illegible]
Stolephorus japonicus [illegible]

Fam. DOROSOMIDAE 149

Fluvialosa richardsoni (Castelnau)
Fluvialosa elongata (Macleay)
Fluvialosa horni (Zietz)
Fluvialosa bulleri Whitley
Fluvialosa paracome Whitley
Nematalosa come (Richardson)

Fig. 3.—Typical species record with illustration and description exposed to view.

the egg and larval stages are known, a red signal denotes a specimen in the reference collection, and a black signal records that an X-ray photograph is on file.

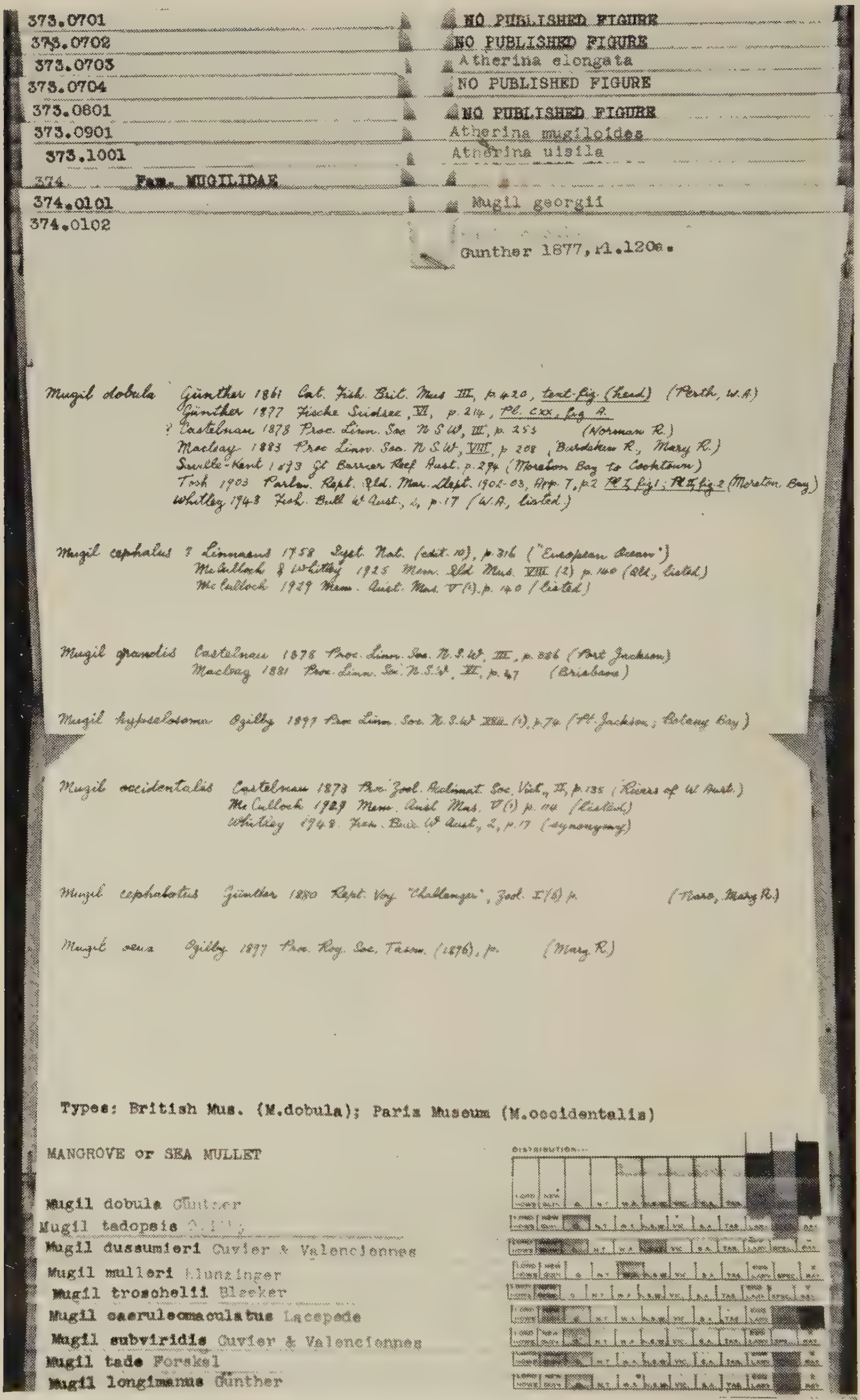
(v) *Habitat.*—Use of marginal inserts in three colours provides a visual guide to habitat. Blue signifies deep-water marine, including oceanic (pelagic or abyssal) and demersal from more than 100 fathoms. Yellow indicates shallow-water, including estuarine and marine littoral down to 100 fathoms. Pink denotes freshwater species. Catadromous and anadromous species are shown in two colours. This is a further reason for dividing the marginal insert into two parts, (*C*) and (*D*).

(vi) *Specific Characters.*—A brief diagnosis is provided on the upper surface of the folded card (*A*,*A*′). This is typed and is available for reference directly below the illustration of the species. Formulae are employed wherever possible.

(vii) *Illustration.*—The back of the preceding pocket provides accommodation for an illustration on the U-cut card (*B*). The illustration is obscured when the folded data card (*A*,*A*′) is opened back in order to consult references. Illustrations are photographic prints, sketches, tracings, and clippings from spare numbers of scientific publications. When it is desired to illustrate male, female, young stages, eggs, and larvae, the supplementary illustrations are mounted beneath the main illustration, using a hinge of cellulose tape. With every figure is an indication of its source and the name under which it was published. This information is provided on a white, folded paper insert (*E*) placed over the right upper corner of the illustration card. The scientific name is indicated in red and below it a source reference in black. Where no published figure is available a plain, white card is substituted. This card bears the words "No published figure" and is available for a sketch or photograph, which would then be designated "Manuscript figure". Also included on illustration cards are notes relevant to length, locality, type, registration number.

(viii) *Synonymy and References.*—The inside surfaces of the folded data card (*A*,*A*′) are reserved for the listing of references and synonyms. When space is inadequate, an overriding sheet (*A*″) is placed over the main card. Standard taxonomic notation is used for recording the references, which are accompanied by specific locality records. All references to Australian records are included in the list together with certain other key references to good descriptions and illustrations of the species. Extralimital references are chosen principally from recent revisions. The cards are faint-ruled and all references handwritten to facilitate additions without removal of the card from its pocket. Generic and specific names included on this card can be located by means of the cross-index.

(ix) *Location of Type Specimens.*—The institutes at which type specimens are located and registration numbers are indicated along the lower margins of folded data cards, immediately above the marginal inserts.



373.0701 NO PUBLISHED FIGURE
373.0702 NO PUBLISHED FIGURE
373.0703 Atherina elongata
373.0704 NO PUBLISHED FIGURE
373.0801 NO PUBLISHED FIGURE
373.0901 Atherina mugiloides
373.1001 Atherina uisila
374 Fam. MUGILIDAE
374.0101 Mugil georgii
374.0102

Gunther 1877, Pl.120a.

Mugil dobula Günther 1861 Cat. Fish. Brit. Mus III, p.420, text-fig. (head) (Perth, W.A.)
Günther 1877 Fische Südsee, VI, p. 214, Pl. CXX, fig. A.
? Castelnau 1878 Proc. Linn. Soc. N.S.W., III, p. 253 (Norman R.)
Macleay 1883 Proc. Linn. Soc. N.S.W., VIII, p. 208, (Burdekin R., Mary R.)
Saville-Kent 1893 Gt. Barrier Reef Aust. p.294 (Moreton Bay to Cooktown)
Tosh 1903 Parlm. Rept. Qld. Mar. Dept. 1902-03, App. 7, p.2 Pl. I, fig.1; Pl. II, fig.2 (Moreton Bay)
Whitley 1948 Fish. Bull. W. Aust., 2, p.17 (W.A., listed.)

Mugil cephalus ? Linnaeus 1758 Syst. Nat. (edit. 10), p.316 ("European Ocean")
McCulloch & Whitley 1925 Mem. Qld. Mus. VIII (2) p.140 (Qld., listed)
McCulloch 1929 Mem. Aust. Mus. V (1). p. 140 (listed)

Mugil grandis Castelnau 1878 Proc. Linn. Soc. N.S.W., III, p. 386 (Port Jackson)
Macleay 1881 Proc. Linn. Soc. N.S.W., VI, p. 47 (Brisbane)

Mugil hypselosoma Ogilby 1897 Proc. Linn. Soc. N.S.W. XXII (1), p.74 (Pt. Jackson; Botany Bay)

Mugil occidentalis Castelnau 1873 Proc. Zool. Acclimat. Soc. Vict., II, p.135 (Rivers of W. Aust.)
McCulloch 1929 Mem. Aust. Mus. V (1) p. 114 (listed)
Whitley 1948. Fish. Bull. W. Aust., 2, p.17 (synonymy)

Mugil cephalotus Günther 1880 Rept. Voy. "Challenger", Zool. I (6) p. (Tiaro, Mary R.)

Mugil [illegible] Ogilby 1897 Proc. Roy. Soc. Tasm. (1896), p. (Mary R.)

Types: British Mus. (M.dobula); Paris Museum (M.occidentalis)

MANGROVE or SEA MULLET

Mugil dobula Günther
Mugil tadopsis [illegible]
Mugil dussumieri Cuvier & Valenciennes
Mugil mulleri Klunzinger
Mugil troschelii Bleeker
Mugil caeruleomaculatus Lacepede
Mugil subviridis Cuvier & Valenciennes
Mugil tade Forskel
Mugil longimanus Günther

Fig. 4.—Typical species record with data card folded back to reveal references.

(x) *Cross-index Number.*—An identification number is allotted to every species to facilitate cross-indexing. This number is typed in black on a small, white, folded paper insert (*F*). The insert is placed over the left upper margin of the illustration card (*B*). The numbers are visible as a list only when the pockets in a tray are reversed.

IV. CROSS-INDEX

(*a*) *Identification Numbers*

Name combinations employed as index markers in the visible margins of species cards in the catalogue are subject to periodic revision. Since these names are variable, they cannot be used as a medium of identification for cross-indexing. As a substitute, identification numbers are allotted to each species. These numbers are not always affected by name changes, but should rearrangement be necessary, a minimum of labour is involved in the readjustment of numbers on cross-index cards.

(*b*) *Decimal Notation System*

Identification numbers allotted to species cards are composed of the basic family number and a four figure decimal. The first two points of decimals refer to the genus and the last two points to the species. This allows for up to 99 genera in each family and 99 species in each genus. The genera are numbered .01--, .02--, .03--, etc. according to their sequence in each family. The species are numbered .--01, .--02, .--03, etc. according to their arrangement in each genus. As example we find:

148	Fam. DUSSUMIERIDAE
148.0101	*Dussumieria hasseltii*
148.0102	*Dussumieria acuta*
148.0201	*Etrumeus jacksoniensis*
148.0301	*Stolephorus robustus*
148.0302	*Stolephorus delicatulus*
148.0303	*Stolephorus japonicus*

(*c*) *Generic and Specific Names*

A cross-index on rotary-mounted cards assists in the location of species from known name combinations. This is essential owing to the non-alphabetic filing arrangement of genera and species in the catalogue and the complicated synonymy of many species. Names are listed on the cross-index cards together with the identification number of the species to which they refer. Cards are salmon in colour and are typewritten in black with headings in red. Every name combination is listed on two cards, being indexed on one under genus, and on the other under species. Generic names are distinguished by upper case and specific names by lower case letters. Subgenera are treated as genera. Tautonymic combinations are listed on genus cards only. Cards are filed alphabetically. Names in the lists are not in alphabetic order since normally less than 10 entries appear under a heading, and new entries can be added to cards without necessitating complete retyping to maintain sequence. As an example of complementary cards we find:

ENGRAULIS	
australis	150.0101
carpentariae	150.0201
antipodum	150.0101
nasutus	150.0301
setirostris	150.0401
scratchleyi	150.0501
grayi	150.0502
antarcticus	150.0101
hamiltoni	150.0502

australis	
ENGRAULIS	150.0101
ELOPS	131.0101
GULARUS	131.0101
ATHERINA	150.0101
AUSTRANCHOVIA	150.0101
GEOTRIA	7.0201
GALEUS	63.0701
GALEORHINUS	63.0701
RAJA	77.0101

(*d*) *Common Names*

Another cross-index on rotary-mounted cards assists in the location of species from any known common name. Cards are green in colour and are typewritten. Names are listed with identification numbers of the species to which they refer. Card headings are restricted to substantive names only, and adjectival components of binary names are listed thereunder. Complementary cards do not occur. As with scientific names, alphabetic sequence is not followed within the lists. Cards are arranged alphabetically.

(*e*) *Family Names*

For location of families a third cross-index of rotary-mounted cards is used. The cards are blue and data are typewritten in black capitals. The accepted family names are listed with their respective identification numbers. Alternative names are indicated as synonyms. Cards are filed in alphabetic sequence.

(*f*) *Literature*

A fourth cross-index on rotary-mounted cards provides a list of ichthyological literature dealing with the area. The cards are yellow and the data typewritten. References listed in the catalogue are quoted in the international system of abbreviations. They are supplemented in the cross-index by a full citation of author, date, title, and reference. A card is allotted to each paper and cards are filed primarily in alphabetic sequence under authors, and secondarily in chronological order under dates of publication. A card is not added until the contents of the article concerned have been extracted and catalogued. This provides a guide to progress in cataloguing.

THE NEW SOUTH WALES TIGER FLATHEAD, *NEOPLATYCEPHALUS MACRODON* (OGILBY)

I. BIOLOGY AND AGE DETERMINATION

By The Late W. S. Fairbridge*

(*Manuscript received September* 11, 1950)

Summary

In a previous paper the catch statistics of the east Australian trawl-fishery (Fairbridge 1948) were discussed, and in the present work, the biology of the most important species, the tiger flathead, is examined in greater detail. An age determination technique is developed for this species, and the age composition of the catch of recent years is analysed.

The sampling technique carried out at the Sydney Fishmarkets is described and tested. The results are given of the first experimental trawling in Australian waters using a fine-meshed cover on the codend.

The biology of the species is studied, chiefly from the point of view of establishing the age determination technique and the final analysis of the catch. Spawning is protracted, lasting throughout the six warmer months, and takes place throughout the geographical range of the species. The males spawn first in their second year, the females in their third or fourth. The "condition" (K) of the gutted fish is lowest in February, after spawning. It is probable that there is a single, genetically uniform stock, with a single centre of maximum occurrence. The younger age-groups probably do not undertake extensive coastwise movement; as a result, local areas are liable to become relatively depopulated by heavy fishing.

The method of collecting and reading the flathead otolith is described. The otolith is found to grow isauxetically above a fish-length of 10 cm., and the technique of back-calculation is therefore used as an aid in age determination. The otolith in this species is certainly not as clear to interpret as that of the North Sea plaice, but is probably comparable with that of the cod or hake.

I. Introduction

The biological investigation of a fishery falls under two main headings: the strictly biological aspect, and the analysis of catch statistics. The two are interdependent, and considerable risks are involved if conclusions concerning the condition of the stock of fish, or the desirable fishing intensity, are drawn from one without a full investigation of the other. In the present instance, the catch statistics for the trawl fishery of New South Wales were treated as a separate study (Fairbridge 1948), and conclusions relating to overfishing were drawn. These were thought to be sufficiently serious to be published as a matter of urgency. The present paper is the biological complement of that work on catch statistics. Though the material presented here was not sufficiently complete for publication then, the general biological picture was there, and was constantly in mind in writing the former paper.

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* Before his death in May 1950, Wolfe Fairbridge studied extensively the trawl-fishery of the east Australian coast. He concentrated his attention particularly on the tiger flathead (*Neoplatycephalus macrodon*) and prepared a very comprehensive paper summarizing the whole of his results. It has been found necessary, for editorial reasons, to publish this in two parts. Part I deals with the biology of this species and the method of age determination adopted. Part II deals with the age composition of the commercial catch, the overfishing of the stocks, methods of conservation, and future research, and will appear in a future number of this Journal.

In the final editing of the paper, which was done after the author's death, many of the more detailed tables, which included the data from which the graphs were prepared, were omitted. These tables are all available and may be consulted at the headquarters of the Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

In the 1920's, tiger flathead (*Neoplatycephalus macrodon*) constituted about nine-tenths of the total annual catch by the New South Wales trawlers. In the following decade, the proportion had dropped to around three-quarters. To-day, flathead constitutes one-seventh of the total catch of 14 million lb., and the bulk of the catch is made up from morwong (*Dactylopagrus macropterus* Bloch and Schneider) and nannygai (*Trachichthodes affinis* Günther). The 1949 wholesale prices of these two species were respectively 10d. and 8d. compared with 1/1d. per lb. for flathead. Morwong and nannygai are caught almost exclusively by steam trawlers, while flathead is more important to Danish seiners.

Though the catch of flathead today is small compared with that of either nannygai or morwong, the past importance of the flathead suggests that it is the species that would best repay study.

Age studies, leading to age analysis of the commercial catch, were carried out to yield the most directly valuable results for conservation. This approach requires also an examination of the biology of the species. Colefax (1934, 1938) studied the general biology of the flathead in 1930 and 1931. The present work is based on fuller sampling, and little of the ground covered by Colefax is duplicated here.

Some important sections of the flathead's biology remain to be worked out, especially the identification of the eggs and larvae, and a study of their distribution and that of the very young metamorphosed stages.

The extent of the New South Wales trawl fishery is discussed in Part II of this paper but Figure 1 shows a map of the south-east Australian coast where the tiger flathead occurs.

(*a*) *The Sampling Technique*

Most of the material treated in this paper was obtained at the Sydney Fishmarket. Considerable numbers of length measurements, weights, and gonad observations are available for 1938 and 1939. A full sampling programme was undertaken by a market measurer of the State Fisheries Department in 1941. This was interrupted from February 1942 until May 1945 because of war service. At first, only lengths were measured, but in January 1946 otoliths, and in May 1946 weight and gonad observations were included. A small collection of otoliths is available from 1941.

Some important sources of extra material are catches of very young flathead made in 1947 and 1948 with a small otter trawl (80 ft. headrope)

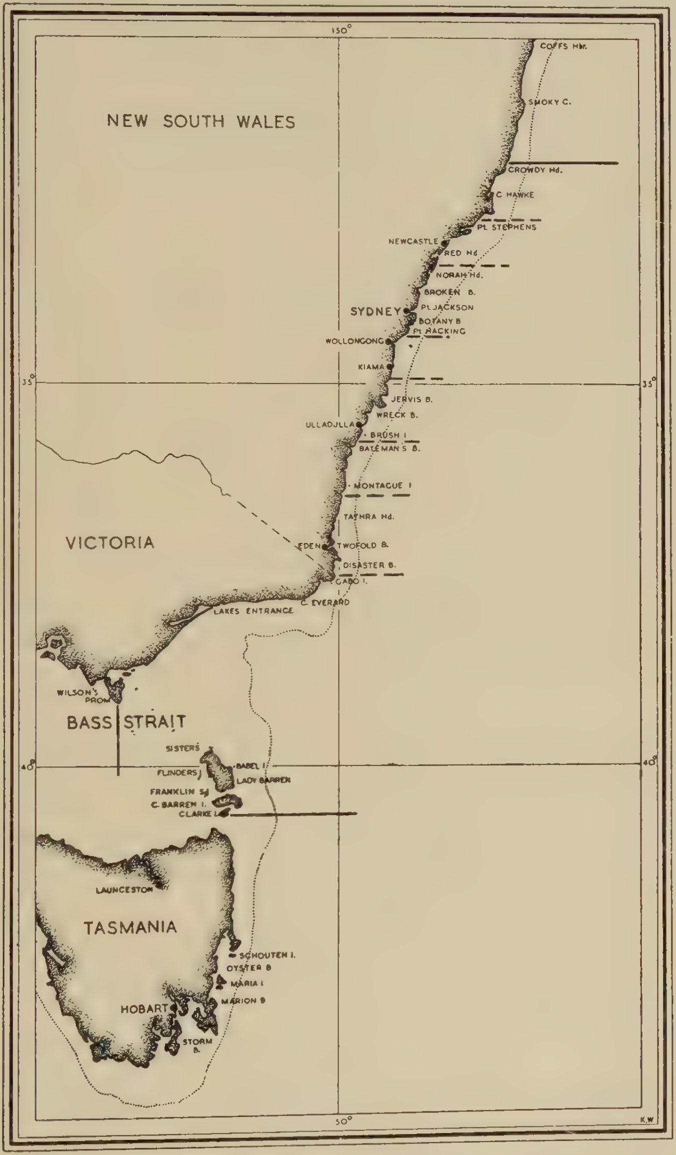

Fig. 1.—The area of the east Australian trawl fishery, approximate limit of the continental shelf, and places mentioned in the text. The heavy black lines indicate the approximate limits of the main flathead fishery; the broken horizontal lines indicate the limits of the areas mentioned in the text.

fitted with fine-meshed codend cover, and a considerable body of general data collected in south-east Tasmania, largely in 1944 and 1945.

Roughly, the programme aimed at in the Sydney Fishmarket from 1946 was to make each month 4,000 random length measurements; to weigh each week 25 fish whole and gutted, the gonad stage being noted and the gonads weighed and otoliths taken. One or two more random samples of otoliths were taken to bring the total to approximately 100 a week. In practice, it was not possible for the measurer to keep to this plan exactly. The numbers sampled for length and otoliths each year are given in Table 1, where the samples are dissected into the main localities of origin.

TABLE 1

TEST OF EFFICACY OF SAMPLING: NUMBERS OF LENGTH MEASUREMENTS AND OTOLITHS TAKEN, AND TOTAL CATCH, FOR EACH MAIN FISHING AREA

Areas	1946 (6 months only)	1946-47	1947-48	1948-49
Port Stephens-Newcastle				
Lengths	30	678	882	844
Otoliths	90	—	105	—
Annual catch (lb.)	124,000	339,000	151,000	132,000
Broken Bay-Port Hacking				
Lengths	1,961	2,298	4,521	1,110
Otoliths	246	410	230	25
Annual catch (lb.)	830,000	605,000	376,000	174,000
Jervis Bay-Brush I.				
Lengths	2,477	3,253	3,120	4,046
Otoliths	398	333	357	149
Annual catch (lb.)	1,251,000	475,000	262,000	253,000
Tathra Head-Disaster Bay				
Lengths	5,114	6,497	6,841	4,828
Otoliths	625	732	260	192
Annual catch (lb.)	1,481,000	1,007,000	597,000	331,000
Trawlers				
Lengths	941	18,583	15,315	8,491
Otoliths	90	2,024	1,038	1,218
Annual catch (lb.)	1,229,000	1,964,000	1,946,000	894,000
Others				
Lengths	4,404	10,350	9,857	5,907
Otoliths	475	764	174	70
Annual catch (lb.)	406,000	585,000	422,000	276,000
Totals				
Lengths	14,927	41,659	40,536	25,226
Otoliths	1,933	4,263	2,164	1,654
Annual catch (lb.)	5,321,000	4,975,000	3,754,000	2,060,000

Marketing practice has varied somewhat during the study, and to understand the nature of the sampling it will be best to treat the changes in marketing practice for the trawler catch separately from those of the Danish seiners.

(i) *Sampling the Trawler Catch.*—The trawler catch is all landed at Sydney. Sampling is therefore a simple matter, and may be considered random and fully representative. Good statistics are available of the monthly landed quantity of each species, but the exact locality of catch is unknown.

(ii) *Sampling the Danish Seiners' Catch.*—These catches are landed at 12 or 15 ports along the coast. In the 1938-42 period, virtually all the catches were trucked to Sydney and passed through the markets. From 1945 onwards, however, considerable quantities were diverted from the Sydney market. The quantities diverted vary somewhat as the distance from Sydney. Much of the Eden catch, for instance, today goes to Victoria or inland in New South Wales. At Newcastle and Wollongong there are local markets where much of the catch is sold.

The owners of Danish seiners are required to supply a monthly return, showing their catch and the port(s) from which they worked. It is safe to conclude that a Danish seiner's catch comes from within a 20-mile radius of its port. When the measurer samples a box of fish at the markets, he is able to ascertain the name of the vessel from which it came. Hence the locality of origin of the Danish seiners' samples can be determined (exceptions being those boats that worked from more than one port in the month, or failed to supply monthly returns).

(iii) *Efficacy of the Sampling.*—In Table 1 the approximate numbers of specimens measured and sampled for otoliths have been arranged according to year and locality (omitting two minor localities) against the total quantity of flathead caught at each locality in each year. By arranging the table in this way the proportion of the samples from each locality may be compared with the proportion of the total commercial catch from that locality. The samples listed under "others" are mostly those from Danish seiners for which no locality record is available.

Serious errors would arise in the final analyses of the age composition of the commercial catch if there were large differences of fish size or growth rate between localities. The extent of these differences is examined later, and is found to be small. The most important is a consistent difference in the length frequency distribution of the trawlers' flathead catch and the Danish seiners' catch.

(*b*) *Experimental Trawling using a Covered Codend*

In view of the interest attaching to this work, the first of its kind done on this coast, it seems best to include a detailed account. Table 2 gives a list of the stations worked (excluding foul shots), the numbers of flathead caught in each shot, dissected into age groups, and the approximate abundance of four other fish species that have particular significance.

The trawling was carried out from the *"H.C. Dannevig"*, a wooden, 75 ft. motor fishing vessel, using a small otter trawl of 70 ft. headrope (a trawl of 80 ft. headrope was used after March 12, 1948) and fitted

TABLE 2

EXPERIMENTAL TRAWLING BY "H. C. DANNEVIG" USING A COVERED CODEND: LIST OF STATIONS AND QUANTITIES OF FLATHEAD AND FOUR OTHER SPECIES TAKEN

Date	Locality	Depth (fathoms)	Bottom	Nos. of Flathead, in Age-groups					*Apogonops*	Juvenile Nannygai	Cucumber Fish	*Argentina*
				O+	I+	II+	III+	Over III+				
6. vi.47	Wata Moli			1	34	4	—	—	?		?	?
19. vi.47	Wata Moli	63	m	3	26	4	—	—	4 Baskets	Common	Common	Rare
2. vii.47	Wata Moli	60	m	—	14	42	15	2	1 Basket	Few	Common	—
2. vii.47	Wata Moli	50	m	Catch lost: contained many I+ & II+ flathead					*c.* 6 Baskets	?	?	?
9. vii.47	Wata Moli	43	m	—	7	5	—	—	3 Baskets	—	Common	Rare
5.viii.47	Montague South	65		—	6	5	1	1	—	Common	Rare	Rare
6.viii.47	Twofold Bay	38	m	—	17	13	—	—	—	Common	Rare	Few
6.viii.47	Haystack R. Beach (Eden)	25	c.s.	—	112	18	3	—	—	1½ Baskets	—	—
6.viii.47	Twofold Bay	30	m	—	146	9	—	—	—	1½ Baskets	—	—
7.viii.47	Gabo I.	53		—	—	2	—	—	—	2 Baskets	Common	Rare
7.viii.47	Twofold Bay	65	c.s. & sh.	—	—	—	—	—	—	—	26 (Spawning)	—
10.viii.47	Wreck Bay	64	c.s. & sh.	—	3	2	1	—	—	—	Few	—
11.viii.47	* Shoalhaven Bight	25	c.s. & sh.	—	8	—	—	—	—	—	—	—
12.viii.47	Wata Moli	30	f.s.	—	3	—	—	—	¾ Basket	Few	—	—
13.viii.47	Broken Bay	24	sh. & gr.	—	—	—	—	—	—	¼ Basket	—	—
13.viii.47	Red Head (Newcastle)	38	m	—	5	28	—	—	4-5 Baskets	Common	—	Few
19. xi.47	Wata Moli	55		—	—	—	—	—	Common	3	16	—
2. xii.47	Wata Moli	30		—	2	1	—	—	2 Baskets	—	—	—
7. xii.47	Jervis Bay	30		—	2	3	1	—	1/10 Basket	—	—	—
11. ii.48	Red Head (Newcastle)	35		1	28	29	—	—	Common	Common	11	—
2. iii.48	Wata Moli	20	s.	—	4	—	—	—	—	—	—	—
4. iii.48	Twofold Bay	45	s.	—	1	15	15	18	90	33	2	—

TABLE 2 (*Continued*)

Date	Locality	Depth (fathoms)	Bottom	Nos. of Flathead, in Age-groups 0+	I+	II+	III+	Over III+	*Apogonops*	Juvenile Nannygai	Cucumber Fish	*Argentina*
4. iii.48	Haystack R. Beach (Eden)	27	f.s. & sh.	—	15	33	8	—	—	2-2½ Baskets	—	—
8. iii.48	C. Everard	32	gr.	—	—	—	—	—	—	—	—	—
9. iii.48	Twofold Bay	55	s. & gr.	—	4	19	12	4	75	2	—	—
9. iii.48	Twofold Bay	30	s. & m.	—	24	31	2	2	—	2½-3 Baskets	—	—
10. iii.48	Green Cape	47	s. & gr.	—	—	—	—	—	45	—	—	—
11. iii.48	Tathra Head	35	c.s.	—	—	3	1	1	—	1/3 Basket	—	—
12. iii.48	Jervis Bay	37	f.s. & sh.	—	140	31	—	—	—	2	—	—
8. x.48	Jervis Bay	43	f.s.	—	—	31	—	—	—	—	—	—
9. x.48	Wreck Bay	64	s.	—	2	12	7	—	Rare	—	Few	—
10. x.48	Montague North	65	s.	—	—	5	2	—	—	—	?	Rare
10. x.48	Montague South	47	s.	—	4	14	—	2	—	Common	—	—
12. x.48	Haystack R. Beach (Eden)	28	s. & sh.	—	3	4	3	1	—	Fairly common	—	—
12. x.48	Twofold Bay	55	c.s. & st.	—	—	—	—	—	—	—	Common	Rare
12. x.48	Twofold Bay	28		—	22	5	6	1	—	Fairly common	Common	Rare
14. x.48	Green Cape	53	s. & st.	—	1	—	3	7	—	—	Rare	—
14. x.48	Tathra Head	35	c.s.	—	—	—	—	—	—	Rare	—	—
15. x.48	Shoalhaven Bight	28	c.s.	—	—	18	13	9	Fairly Common	—	—	—
16. x.48	Wata Moli	35	m	—	4	4	—	1	Common	Rare	—	—
16. x.48	Wata Moli	60	m	—	1	10	—	2	Fairly common	Rare	Common	—
20. x.48	Broken Bay	25	c.s. & st.	—	—	—	—	—	—	1 Basket	—	—
21. x.48	Red Head (Newcastle)	30	f.s.	—	11	20	7	1	Very rare	Common	—	—
21. x.48	Red Head (Newcastle)	66	m	—	—	—	—	—	—	—	3	—
23. x.48	Broughton I.	41	f.s.	—	5	19	7	7	Fairly common	—	—	—

TABLE 2 (*Continued*)

Date	Locality	Depth (fathoms)	Bottom	Nos. of Flathead, in Age-groups					*Apogonops*	Juvenile Nannygai	Cucumber Fish	*Argentina*
				O+	I+	II+	III+	Over III+				
23. x.48	C. Hawke	36	f.s.	—	—	12	9	13	Rare	—	—	—
24. x.48	Crowdy Head	31	f.s.	—	—	1	7	4	Few	—	—	—
7. xi.48	Jervis Bay	42		—	8	34	9	3	*c.* 300	—	6	—
7. xi.48	Wreck Bay	50		—	—	—	—	—	—	—	4	2
8. xi.48	Haystack R. Beach (Eden)	*c.*27		—	—	—	—	—	—	—	—	—
9. xi.48	Disaster Bay	33		—	22	9	—	—	—	1/10 Basket	?	—
9. xi.48	Green Cape	*c.*55		—	—	—	—	—	—	—	—	—
11. xi.48	Twofold Bay	40		—	—	—	—	—	—	—	¾ Basket	Rare
11. xi.48	Twofold Bay	20		—	16	33	—	—	1	Few	Few	—
12. xi.48	Tathra Head	38		—	—	—	—	—	—	Few	—	—
12. xi.48	Montague South	44		—	—	—	—	11	—	Few	Few	—
13. xi.48	Wreck Bay	*c.*60		—	3	21	8	2	1/10 Basket	—	1/3 Basket	1
13. xi.48	Wata Moli	*c.*25		—	—	—	—	—	Fairly common	Rare	Few	—
13. xi.48	Wata Moli	*c.*60		—	—	—	—	—	¼ Basket	Rare	Rare	—
20. xi.48	Red Head (Newcastle)	36	m.	—	2	—	—	—	—	—	—	—
20. xi.48	Red Head (Newcastle)	68	m.	—	—	14	4	—	½ Basket	—	Few	—
22. xi.48	Port Stephens	65	f.s.	—	—	8	5	3	—	Few	Few	—
15. xii.48	Haystack R. Beach (Eden)	26	f.s.	—	1	18	4	—	—	1	—	—
16. xii.48	* Disaster Bay	43	s.	—	6	168	—	—	—	Few	—	—
18. xii.48	Twofold Bay	50	c.s.	—	10	20	—	—	—	—	Rare	Rare
18. xii.48	* Twofold Bay	40	f.s.	—	14	14	—	—	—	—	—	—
19. xii.48	Wreck Bay	38	s.	—	—	—	—	—	Few	Rare	Rare	Rare
19. xii.48	* Jervis Bay	40	s.	—	6	12	—	—	240	—	4	—
20. xii.48	* Wata Moli	60	s.	—	36	—	—	—	300	—	24	—
20. xii.48	* Wata Moli	17	s.	—	10	—	—	—	—	—	—	—

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* These shots were of ½ hour duration; the numbers shown in the table are double the numbers actually taken.

with V.D. sweeps. The codend of 3¼ in. mesh was enclosed in an outer codend of ¾ in. mesh (measured diagonally from knot to knot). This was towed for one hour, reckoned from the time when all the wire of the warps had been paid out to when hauling was begun. In a few cases the duration was cut by half. The decision to limit hauls to only an hour was made when, in the early part of the work, enormous catches of *Apogonops anomalus* Ogilby were being taken in the codend cover; at this time one codend cover was split by a catch estimated at six baskets of this small fish (July 2, 1947). Every effort was made to keep the hauls comparable over the period.

The entire catch of flathead was always measured. The separation into age groups was done either direct from the otoliths or, in the occasional large catches, by combining age determinations with the length frequencies of the sample.

The flathead and juvenile nannygai were the only commercially valuable species on which regular observations were made. Nevertheless, a rough measure of abundance was made of all species in each haul. Sometimes, depending on weather and the press of work, all the specimens of one species were measured; in this case the actual number is shown in the table. More often, the abundance was indicated by stating "rare", "common", etc., or estimating the quantity in bushel baskets. The word "rare" indicates less than about six specimens; "few", less than 24; "common", more than 24. These rough categories are shown in the table for four species: *Apogonops anomalus,* juvenile nannygai (*Trachichthodes affinis*), cucumber fish (*Chlorophthalmus nigripinnis*), and *Argentina elongata.*

The stations were at first chosen at random. It soon became evident that the juvenile flathead were concentrated in the water of 35 to 30 fathoms and less. It is a feature of the New South Wales coastline that the bottom within the 30 fathom contour is almost universally rough and untrawlable. The author therefore found himself continually striving to make shots in water as shallow as possible, and actively seeking out the few areas (such as Twofold Bay, Shoalhaven Bight, and Wata Moli) where trawling was possible in relatively shallow water (the ready cooperation of the Master in this rather nerve-racking work is acknowledged here). It was felt at first that the experimental trawling might only be touching the fringe of the flathead nursery grounds. Some trawling was therefore undertaken in Twofold Bay, using a small prawn otter trawl from a power boat, in 15-20 fathoms. No juvenile tiger flathead were taken. At Stockton Bight (Newcastle) professional prawn trawling was being carried out in 1948 in about 5-10 fathoms, and only an occasional juvenile tiger flathead was being taken. While the possibility cannot yet be ruled out of heavy concentrations in less than 25 fathoms, and in areas of the coast untouched by this work, the author feels that a good indication was obtained of the abundance and distribution of the young flathead in these years.

It is difficult to arrive at an exact comparison between years, because of extreme patchiness of the catches. For example, slight differences in depth in the Twofold Bay area produced great changes in the numbers of juveniles taken. The table shows that in the Twofold Bay and Jervis Bay areas in 1947-48 catches of over 100 of the I+ (1946-47 year-group) flathead were made; whereas in 1948-49 the largest catches of the I+ (1947-48 year-group) fish were 22 in the Twofold Bay area (twice) and 36 at Wata Moli, with sometimes very considerable catches of the II+ (1946-47 year-group) fish at many localities (one catch at Disaster Bay was 168). At this stage it would be unwise to stress the differences between year-groups suggested here, but they are worth indicating as suggesting the value of this line of work.

Turning now to the other species listed in the table, *Apogonops* is by far the most important fodder species. It grows to a length of 10 cm. and its young were taken in the codend cover in great numbers down to a length of 1.5 or 2 cm. The table shows that there are two localities—Wata Moli and Newcastle—where this species is particularly abundant; this may perhaps be correlated with the areas of mud bottom found in these localities. In other localities it was almost always present, but was not caught in anything like the numbers at those two localities. This does not rule out the possibility that it is more or less equally abundant all along the coast; it may hug the bottom more in the Wata Moli and Newcastle areas. It is certain, from the table, that until the winter of 1948 *Apogonops* was very much commoner than in the following spring and summer.

It is most interesting that the juvenile nannygai show a similar population fluctuation. Until the winter of 1948, specimens about 5 or 6 cm. long occurred in quantities of a basket or more per hour's shot at more than one locality, but chiefly in the Twofold Bay area. Later in 1948 they were always commonest in the Twofold Bay area, but did not occur in anything like the numbers of the previous year. Moreover, length measurements showed that many of the best hauls obtained in the summer of 1948 were principally of the same year-group as that which comprised the rich hauls of 1947-48. The distribution of the juvenile nannygai closely follows the distribution of the juvenile flathead. Both species were found most commonly in water of less than 30 or 35 fathoms, and the Twofold Bay area seemed to be a special nursery ground for each.

The cucumber fish and *Argentina* are recorded because it is felt they may be commoner in other years, and at times important as fodder species. In Tasmanian waters *Argentina* was found to some extent filling the role of *Apogonops* in the flathead diet. Cucumber fish of fair size are reputedly common in very deep water (over 90 fathoms), and these might in the future be commercially exploited. Almost all specimens taken in the present work were juveniles. In this species, there is an obvious correlation both of abundance and size with depth.

II. Biology of the Flathead

(*a*) *Breeding*

(i) *Gonad Maturation Stages and Ova Diameters.*—A table of gonad stages has been drawn up with a departure from usual practice in discarding the males. It was found impossible to distinguish between testes that were increasing in size preparatory to spawning, and partly spent testes; in practice, a field worker tended to classify the males as ripening, ripe, or half-spent, largely on the condition of the females from the same catch. Even running ripe males are no certain indication of spawning; they may be found in this condition for nearly nine months of the year, whereas the period of spawning by the females is much more restricted. Where females are spawning, a particularly high proportion of the males is usually running ripe; but it is the females that supply the indubitable evidence. The stage of the testes is therefore indicated on data sheets simply by the sign II+, to indicate that maturation has at least begun and that they are not in stage I.

The following is the table of female flathead gonad stages used from 1946 onwards:

I.—Immature; sexes indistinguishable. The gonad is a colourless thread of tissue, often difficult to identify at all.

II.—Adolescent. The ovary is quite distinct, short but plump, about the thickness of a pencil, the walls taut, and the whole organ clear and glassy. Though it may not have reached its full thickness, it is always quite distinct from I.

III.—As in II, but yellow. The individual ova cannot be distinguished with the naked eye. These may be immature fish, or recovering females that have spawned at least once before.

IV.—The ova are round, and may be quite clearly made out with the naked eye; the stage covers a wide range of sizes; colours vary from pale yellow to pale orange; the lumen is very evident in the early stages of ripening but disappears in the last stages.

V.—At least some of the yellow, opaque ova of stage IV have increased to several times their former diameter and are clear and glassy; ova cannot be expressed by light pressure.

VI.—Running ripe.

VII.—The half-spent ovary is indistinguishable from stage IV, and this stage therefore remains in practice unfilled.

VIII.—Spent. The ovary is flat, flaccid, appears dark owing to the pigment in the walls, and may be bloodshot (blood may be evident in the ovary at any stage, presumably often a result of the fish being caught, the changes in pressure, and so on); the individual ova cannot be made out with the naked eye, but a few blood-coloured spots are evident which are the large unspawned ova being broken down. This stage grades into III.

Most of these stages are quite distinct macroscopically, one from another, and are identified correctly by a technical assistant in the field. The impossibility of distinguishing between stage IV and half-spent ovaries is a difficulty that will be dealt with more fully below. Another difficulty is the impossibility of distinguishing some of the recovering stage III from an immature stage III. It is also fairly evident that many of the spent (stage VIII) fish go straight to stage IV when they recover, without passing through any recognizable stage III.

To determine the significance of these stages, a microscopic study was carried out. Examples of the various gonad stages were preserved in formalin and subsequently broken up thoroughly by Raitt's (1932) method. The well-separated ova were examined under a binocular dissecting microscope without the need for sectioning or staining. Plate 1 shows photographs of some of this material.

A comparison with previous literature, principally Hickling (1930) and Raitt (1932), makes it possible to classify the ova into four main groups:

Group (*a*).—Very small, angular ova, glassy and colourless; the nucleus is visible even in such crudely treated material, and in the larger specimens a few yolk granules are visible.

Group (*b*).—Not sharply defined from the previous group, but the yolk granules have increased so that the ova begin to appear opaque, though never so dense as to obscure the nucleus, which occupies the greater part of the ovum; they are becoming round and are larger than group (*a*), varying up to about 0.22 mm. diameter.

Group (*c*).—Large round ova, up to about 0.54 mm. diameter, absolutely opaque, yellow; the sizes vary down to group (*b*), but are mostly quite distinct.

Group (*d*).—Very large, round ova, usually distinct from group (*c*) by reason of their size (up to 1.0 mm. diameter), semi-transparent appearance, and loss of yellow coloration; an oil globule is also distinctly visible. These ripe ova have been artificially fertilized and when alive measure 1.0 mm.

The group (*a*) ova are presumably Hickling's "reserve fund eggs"; group (*b*) are reserve fund eggs undergoing development; group (*c*) are developing ova, most of which will presumably be spawned during the coming season; group (*d*) are the large, colourless ova of stage V and VI ovaries, representing the group (*c*) ova that have absorbed water and are approaching complete ripeness, preparatory to being spawned.

The microscopic characters of each gonad stage were established as follows (Plate 1, Figures 1-6, shows photographs of this material, illustrating the four egg groups and some of the gonad stages; Figures 3-6 are all to the same magnification so that the sizes of the ova may be compared):

Gonad stage II.—The contents are all typical group (*a*) ova, with here and there some very early group (*b*) ova, but none larger than 0.08 mm. diameter.

Gonad stage III.—Two specimens examined were from flathead of 42 cm. and 37 cm. length. The former was quite indistinguishable from a stage VIII gonad, save by external appearance, the group (*b*) ova being no more than 0.2 mm. in diameter; the latter ovary contained numerous developing opaque ova (group (*c*)) but none of these was larger than 0.3 mm. diameter (Plate 1, Figs. 1 and 2).

Gonad stage IV.—Egg groups (*a*), (*b*), and (*c*) are present in varying numbers but (*a*) and (*b*) are always numerous, while group (*c*), by reason of their large size (up to 0.6 mm. diameter) fill the greater bulk of the ovaries. Group (*b*) are usually extremely numerous relative to group (*a*) (Plate 1, Figs. 3-5).

Gonad stage V.—Groups (*a*) and (*b*) are present, with group (*b*) very numerous; group (*c*) present in varying numbers and of various sizes; the stage is distinguished by the presence in varying numbers of the very large, round group (*d*), which are quite sharply distinct in size from the largest group (*c*). All the usual intermediate stages between the first three groups are present.

Gonad stage VI.—As for stage V, but the gonad is much larger (unless partially spent), with group (*d*) ova making up the bulk of the organ and lying free in the lumen. Group (*a*), (*b*), and (*c*) ova are confined to a narrow layer inside the ovary wall (Plate 1, Fig. 6).

Gonad stage VIII.—Both groups (*a*) and (*b*) are present; group (*a*) constitute the great bulk of the ovary but group (*b*) are numerous and intermediate sizes not so numerous. In some specimens there are a few large group (*c*) ova undergoing breakdown.

Besides a qualitative examination, this material was examined by making ovum-diameter measurements of representative samples. An effort was made to randomize the measurements so that each ovum group would be represented in approximately the proportion in which it occurred in the sample. Some examples of these ovum-diameter frequencies are illustrated in Figure 2. The group (*a*) ova were not measured since they are far too numerous in all gonad stages.

Figure 2*A* shows the ovum-diameter frequencies of an early stage IV gonad. There is little indication of a separation between the group (*b*) ova and group (*c*). Figure 2*B*, *C*, *D*, and *E* show what appear to be subsequent stages, in order, as the group (*c*) ova grow in size, gradually become separated from the "reserve fund" of group (*b*), and appear to form a stock of ova at a diameter of about 0.45-0.60 mm. These are ready to make the sudden step to group (*d*). Figure 2*F*, *G*, and *H* show stage V and VI gonads with the group (*d*) ova sharply separated from the group (*c*), suggesting that the change at this stage from one group to the next is rapid.

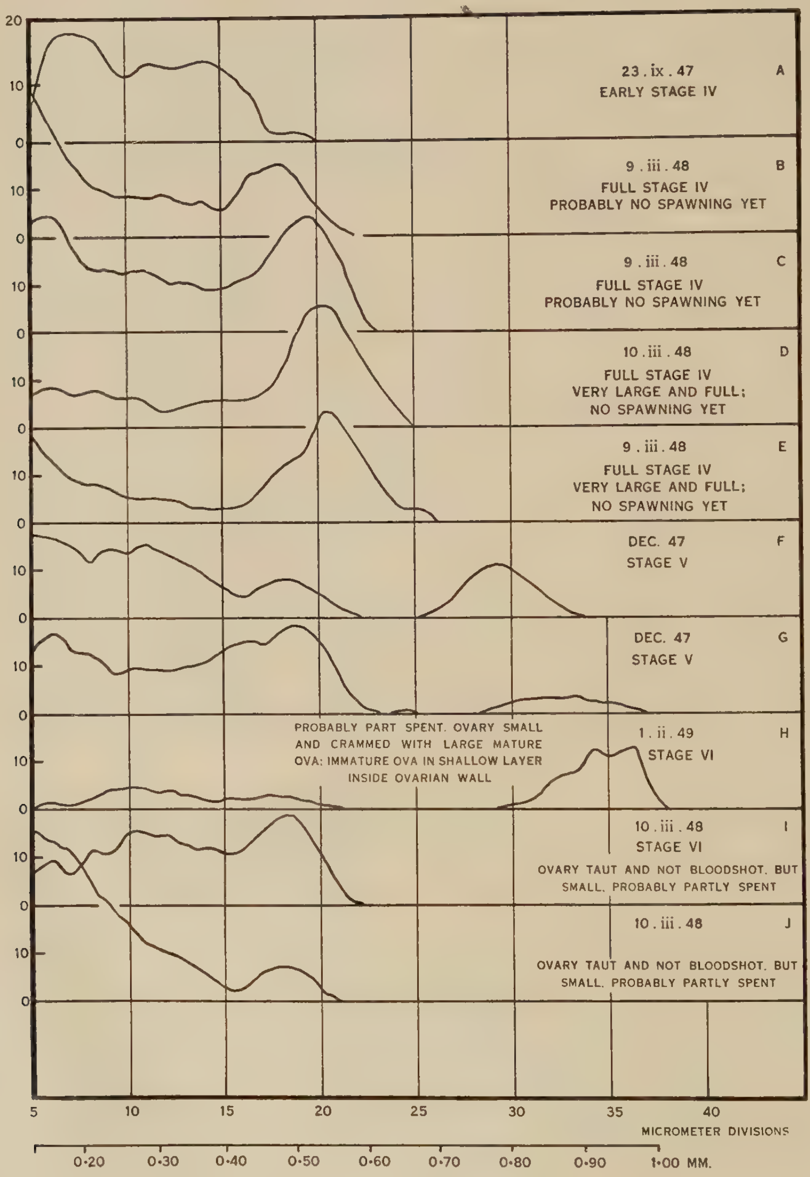

Fig. 2.—Diameter frequencies of intra-ovarian flathead ova, arranged according to their supposed order of maturity. Raw frequencies smoothed by a moving average of three.

Figure 2 strongly suggests that the flathead belongs to the type of fish that does not shed all its eggs at once in a few days, but in two or more batches. It seems quite impossible that the smaller group (*c*) ova of Figure 2*F*, *G*, and *H* should grow and mature in time to be shed along with the already formed group (*d*) ova. The problem has been treated by Clark (1934) and Hickling and Rutenberg (1936). These authors argue that multimodal diameter-frequency curves of developing (group (*c*)) ova indicate that spawn is shed in a series of emissions corresponding with the modes. The comparative rarity of flathead in stages V and VI suggests that once group (*d*) (mature) ova begin to develop, spawning is not long delayed. Therefore, the late group (*c*) ova in Figure 2*F*, *G*, and *H* would be spawned in the current year, but at a later date.

Such an explanation would account for some of the irregularity in gonad stage between samples of flathead, in particular the presence of what appear to be half-full stage IV gonads late in the spawning season; these latter would presumably be partially spent. Two such gonads that appeared from external features to be partly spent—that is, they were small but taut, and definitely not stage VIII, but taken very late in the season along with fish having full gonads—are illustrated in Figure 2*I* and *J*. They show a stock of group (*c*) ova that have not reached the size at which they would be ready to change into group (*d*): in Figure 2*I* the group (*c*) ova are in a very high proportion to the "reserve fund" eggs, in other words, there are many ova yet to be spawned, but in Figure 2*J* there are relatively few, and spawning has apparently been all but completed.

A further corollary from Figure 2 is that estimation of fecundity by the usual means of counting the group (*c*) ova of a representative sample of the ovary is impossible for the flathead. There is no sharp distinction between them and the group below, even at the time when some of the ova are changing over to the group (*d*) stage preparatory to spawning. It is, in fact, a matter of some interest to determine how many of the group (*c*) ova of a specimen such as Figure 2*G* would be matured and spawned in the current season. The largest group (*c*) ova in a stage VIII or recovering stage III gonad is 0.3 mm., so presumably most ova down to that size would be spawned; but this cannot be considered by any means certain, as large numbers of half-developed group (*c*) ova might be broken down if they were not spawned before the end of the season. No alternative means of estimating fecundity has been devised in this species.

(ii) *Spawning and the Seasonal Cycle of the Gonad Stages.*—The Sydney market samples are the chief basis for the work on the seasonal cycle of the gonad stages. It is not necessary to give all this material in detail. To obtain the overall pattern, the year was divided into four periods of three months on the basis of the known spawning habits of the flathead. The proportion of the different gonad stages was noted as follows: In July-September, the proportion of stages IV-VI was rising, of VIII was falling. In October-December, stages IV-VI were common and

VIII was scarce. In January-March, stages IV-VI were rarer, VIII was commoner and in April-June, stages IV-VI were rare and VIII was common.

The mean monthly gonad weights of male and female flathead for three 12-month periods are given in Figure 3.

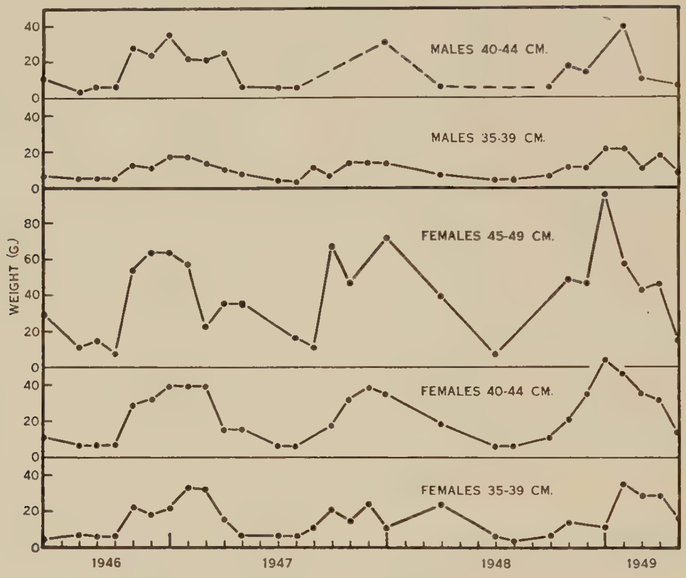

Fig. 3.—Average monthly gonad weights of the flathead. The curves have been drawn by eye, to indicate the general cycle of maturation and spawning.

It can be readily seen that there are high gonad weights throughout the summer months, falling very low in June, July, and August. Irregularities in the summer months are due to sampling the catch from different localities. No one locality could be adequately sampled to give a continuous picture of the changes in that area, because the fishing fleet tends to follow the incidence of spawning fish during the summer. The greater regularity of the weights of the male gonads is due to the more protracted spawning by the males.

During June and July, gonad stages are all II, III, or VIII—i.e. adolescent or spent. It was considered that indubitable evidence of spawning was afforded only by female gonad stages V and VI. These stages are, however, surprisingly infrequent in the commercial catch—an observation confirmed by the author's own experience at sea, and by Colefax (1938). To obtain fuller observations, therefore, the market measurer from 1947-48 onwards recorded the origin of any sample noticed by him in the markets that contained flathead in stages V and VI. In Table 3 the seasonal and locality distribution of the spawning flathead are given, the numbers referring to numbers of samples observed, not to individual fish.

It must be remembered that the catch from the southern and northern areas is not sampled as fully as that from Sydney and Jervis Bay. The absence of positive observations from the Newcastle and Montague Island areas is probably not a true reflection, since spawning has at other times been observed in both areas. Spawning appears to occur in many localities, probably on all trawling grounds, with the possible exception of those deeper than 50 or 60 fathoms. Some observations from south-eastern Tasmania complete the pattern. Though no stage V or VI females were found, there was a sudden change from stage IV to stage VIII females in early May 1944 and late April 1945; the males freely running with milt from about January to May.

Summarizing these observations, it can be said that, in general, spawning begins and ends sooner in the north than in the south, beginning in October and ending about April or May in the extreme south. Colefax's (1938) results confirm this, and numerous verbal reports agree.

TABLE 3

SEASONAL AND LOCALITY DISTRIBUTION OF SPAWNING FLATHEAD

	1946-47								1947-48								1948-49							
Months	S.	O.	N.	D.	J.	F.	M.	A.	S.	O.	N.	D.	J.	F.	M.	A.	S.	O.	N.	D.	J.	F.	M.	A.
Port Stephens — Newcastle	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—		—
Broken Bay — Port Hacking	—	—	—	3	2	—	1	—	—	1	2	6	—	—	—		—	—	—	1	—	1		—
Wollongong — Kiama	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—		—	—	—	—	—	—		—
Jervis Bay — Brush I.	—	—	1	1	—	—	—	—	—	—	3	2	4	1	1		—	—	—	2	2	1		—
Bateman's Bay — Montague I.		—	—	—		—	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—		—
Tathra Head — Disaster Bay	—	—	—	—	—	1	—	—	—	—	—	—	—	3	4		—	—	—	—	—	—		—
Unknown Origin (steam trawler catch)	—	—	—	—	1	1	1	1	1	—	—	4	1	5	2		—	—	—	2	—	2		—

Associated with spawning is a well-established inshore migration and a tendency to shoal up, which makes for good fishing. It is therefore interesting to notice a gradual shift in emphasis of the fishing from north to south during the summer months (Fig. 9). The "Botany Glut" appears to have been a spawning concentration lasting from September to December or February, with spawning in December. Fishermen are agreed that good fishing does not start at Eden until January. From private reports, it appears that the flathead came into the Lakes Entrance (Victoria) grounds in particular numbers in 1948 from January to March, and this appears therefore to have been a spawning movement.

(iii) *Length and Age at First Maturity.*—Table 4 summarizes the 1946 and 1947 data on the length of the flathead at first maturity. Included in these data is the material obtained by experimental trawling using a fine-meshed cover on the codend. The table is not taken below a fish-length of 19 cm., since all specimens below this size were in gonad stage I and of indeterminate sex.

These length frequencies should be compared with Table 8, where the number of flathead of each cm. group is arranged in age-groups. It will be seen that gonad stage II, which shows the first onset of maturation, agrees with II+ age-group. Stage III has both fish that have not yet spawned, and spent recovering fish. Stage IV length frequencies show a sudden increase at about the 36 cm. size-group, which is the III+ age-group. It is evident that the two-year-old fish of gonad stage II have advanced to gonad stage IV by the following year. The smaller size-groups of stages III and IV, therefore, represent immature fish, while the larger, more numerous specimens of stage III are at least partly made

TABLE 4

LENGTH FREQUENCIES OF FLATHEAD AT FIRST MATURITY

Fish-Length (cm.)	Sex Indeterminate	Males II+	Females Gonad Stages					Total Females
			II	III	IV	V & VI	VIII	
19	—	1	1	—	—	—	—	1
20	—	3	—	—	—	—	—	—
21	—	4	2	—	—	—	—	2
22	1	3	11	—	—	—	—	11
23	—	20	8	—	—	—	—	8
24	1	19	13	1	—	—	—	14
25	1	27	10	—	—	—	—	10
26	2	29	18	5	—	—	—	23
27	4	42	26	4	1	—	—	31
28	3	36	18	8	—	—	—	26
29	1	21	13	4	2	—	1	20
30	—	20	11	3	3	—	3	20
31	1	28	11	3	2	—	2	18
32	2	33	5	4	2	—	3	14
33	—	39	4	3	3	—	3	13
34	—	33	1	4	7	—	6	18
35	—	40	1	3	5	1	10	20
36	—	45	2	9	10	—	13	34
37	—	35	1	5	15	—	15	35
38	—	28	—	16	39	—	17	72
39	—	40	—	26	31	3	8	68
40	—	28	—	21	40	7	22	90
41	—	29	—	11	32	3	13	59
42	—	26	—	15	32	3	18	68
43	—	26	—	6	20	3	4	33
44	—	13	—	3	19	5	5	32
45	—	15	—	2	22	4	5	33
46	—	10	—	2	13	4	3	22
47	—	12	—	1	14	3	2	20
48	—	7	—	—	13	1	5	19
49	—	1	—	2	9	2	3	16
50	—	—	—	1	3	—	1	5

up from spent recovering fish. The meagre length frequencies of the spawning females support the conclusion that the female flathead does not spawn before its third summer (III+ fish), and some of them perhaps not till the fourth.

Maturing but still virgin males cannot be distinguished with any certainty from some later stages. The running ripe stage, however, though discarded as a reliable indication of spawning, does provide the most direct evidence of size at first spawning. In contrast to the females, this stage in the males is very common. Some material taken in 1938-40 has been grouped into 3 cm. size-groups and the summarized data, up to the 39-41 cm. group, are given in Table 5. Though these gonad stages are not now used, stage VI can be certainly taken as running ripe, while stages IV, V, and VII would represent well-developed gonads. The stage I specimens are marked "indefinite".

TABLE 5

GONAD STAGES OF MALE FLATHEAD

Size-groups (cm.)	Gonad Stage							
	I	II	III	IV	V	VI	VII	VIII
22	—	—	—	—	—	—	—	—
25	1	1	—	—	—	—	9	5
28	—	2	1	—	1	13	123	17
31	4	4	7	1	1	31	148	16
34	—	3	3	—	1	20	167	66
37	—	—	—	—	—	19	109	54
40	—	—	—	—	2	18	68	29

It seems evident from these figures that virtually all the males in the commercial catch are sexually mature. Taking these figures in conjunction with Table 4, it seems reasonable to deduce that in male fish from a size of about 20 cm. the gonads are maturing, and that spawning takes place first at a length of 28 or 30 cm. Reference to Figures 21 and 22 shows that maturation begins, therefore, in the late I+ males, and first spawning follows in the ensuing summer, when the males are aged II+.

Summarizing, gonad maturation in the females begins in the II+ age-group, and spawning takes place for the first time one or two years later when the females are III+ or IV+; in the males, the gonads begin to mature when the fish are I+ and they spawn first when they are aged II+. The legal minimum length of 13 in. (33 cm.) therefore protects the majority of the males till they have spawned once, but permits considerable inroads to be made into the stock of females before spawning has occurred.

(iv) *Ratio of the Sexes.*—The proportion in which the sexes occur in the flathead catch departs from a simple 50 : 50 ratio and merits some study. The proportion of the sexes at each age- and size-group in samples of the commercial catch of a fish species evidently depends on several factors: the proportion in which the sexes first hatch from the egg and their viability before sexual maturity; differences in the growth rate of the sexes and in their age (or size) at first maturity; shoaling habits before and after maturity and consequent differential effects of fishing; and viability after the onset of sexual maturity. The actual numbers of each sex in the commercial flathead catch are shown in Figure 4.

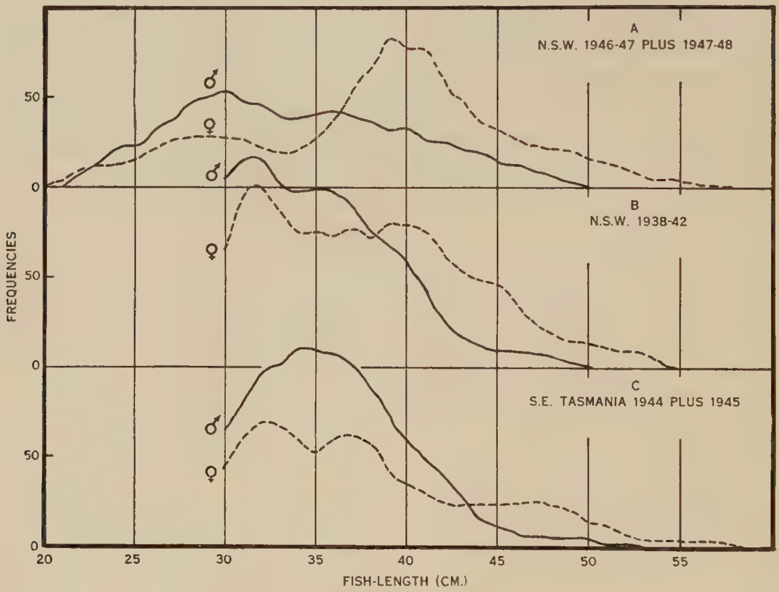

Fig. 4.—*A-C*, Length frequency curves of the flathead dissected into sexes; smoothed by a moving average of three, and the curves drawn by eye. *A*, market material of 1946-47 and 1947-48, plus material from experimental hauls using a covered codend. *B*, market material of 1938-42. *C*, material obtained in south-eastern Tasmania. *A* has been arbitrarily commenced at a fish-length of 20 cm., and *B* and *C* at a length of 30 cm.

In Figure 4*A* the market material of two years has been augmented in the lower size-groups by including the material derived from experimental fishing using a covered codend. The sexes may be clearly distinguished by the naked eye down to a length of 15 cm., but actually very few specimens were taken of 15 to 20 cm. length. Below about 15 cm., identification of the sexes becomes uncertain. The early market samples of 1938-42 have been plotted in Figure 4*B* as a check against the more recent material. The material from south-eastern Tasmania, which was obtained during commercial fishing tests with an ordinary Danish seine, is plotted in Figure 4*C*.

The flathead is clearly a typical case in which the males predominate in the lower size-groups but then fall away in numbers, leaving the females predominant. Figure 4*B* seems to depart from this somewhat in the lower size-groups, but the high proportion of females at 31-33 cm. is due to a single large sample of small fish containing a high proportion of females. In the New South Wales samples the point at which the females overtake the males is between 36 and 39 cm.

The Tasmanian material is interesting, since it represents the condition in what is presumably a virgin fishery. Here the early preponderance of males is of about the same order as in the New South Wales samples but persists up to a size of 5 or 6 cm. greater. The drop in numbers of the males is equally sudden and begins at about the same size, namely 37 cm.

The difference in growth rate of the sexes will be dealt with (Section III (*c*) (iii)); it is not great, and can be disregarded here. The differences in age at onset of maturation and at first spawning are, however, important. From the preceding section, males of 30-35 cm. are probably all sexually mature and those down to 20 cm. are mostly maturing. The females, however, do not spawn until they are about 34-35 cm. and larger. Experimental trawling has demonstrated that O- and I-group flathead do not occur on the trawling grounds but live mostly inside the 30-fathom contour. These age-groups, therefore, are virtually protected from the fishery. It seems probable that the changing ratios of the sexes illustrated in Figure 4 may be explained as follows: Assuming that the sexes are in equal proportions in the young fish, it appears that the males with maturing gonads tend to move out from shallow water onto the main trawling grounds and dominate the catch of the 25-35 cm. size-groups. When the females, in their turn, begin to mature there is an influx of this sex, and not only the proportion, but the actual numbers, of females rise after about 35 cm. The influx of maturing females is not sudden but takes place gradually throughout the year. If the influx of the females were a spawning behaviour, one would expect it to be sudden; but the fish-length at which it occurs and its progressive nature are evidence that it is associated with the gradual ripening of the gonads. Further, during the period when the small males preponderate they are being caught disproportionately and in large numbers. (The samples from which Figure 4 was drawn were random, with the exception of Figure 4*A* below 30 cm., and therefore reflect the true proportions of the size-groups taken through the year by the fishery.) It is understandable, therefore, that the females, which have been partially protected for a year should then, in their turn, dominate the fishery.

The discrepancy between the sexes continues in all the graphs roughly to the same degree, and the largest females are considerably larger than the largest males. In fact, it is as if there were two independent population curves, one placed before the other. This explanation accounts for the great preponderance of large females over large males, which Dakin (1939) noticed, and there is no evidence of a higher natural mortality rate in the males nor any need to postulate this to account for the differences.

A high natural mortality is, however, strongly indicated in Figure 4*C*. There had been no fishing in the particular locality since 1940 (see Blackburn and Fairbridge 1946) and, though it is possible that the stock of flathead in south-eastern Tasmania is at least to some extent augmented from the Bass Strait trawling grounds, there had been little or no fishing on these grounds either since 1942. Yet the length frequencies of the male flathead show a very rapid fall from about 35 cm. The right-hand slope of this curve must be very largely a reflection of natural mortality. The relatively low frequencies of the females seem to reflect a severe natural mortality among them also. It is true that this material is derived from the extreme southern limits of the flathead population and may be non-representative; but if it can be taken as truly reflecting the condition over the bulk of the flathead population, there are important corollaries for control of the fishery that are dealt with in a later paper.

(*b*) *The Weight/Length Relationship*

The usual monthly sampling at the fish market provides the bulk of the material for this section. Samples were individually weighed (on a cantilever balance) whole, and gutted; the gonads were also weighed. In addition, weights are available for some of the samples of very small flathead obtained during the experimental trawling using a covered codend. There is also some material from the Tasmanian samples and from the early years 1938-42. Figure 5*A* shows the distribution of the average weight/length values of the New South Wales material of 1946-47, together with the averages of the Tasmanian material; the New South Wales series has been augmented below the 30 cm. size-group with the samples of small flathead obtained experimentally. The figure shows there is no marked difference between the New South Wales and Tasmanian material.

Figure 5*B* shows the New South Wales weights plotted against the cubes of their lengths. The points do not fall exactly on a straight line; the weights of the larger fish are slightly higher in proportion than the weights of the smaller fish (i.e. the larger fish are thicker or their specific gravity is higher). Nevertheless, the relationship is close to a linear one, particularly between the 30 and 50 cm. size-groups. These size-groups were the most abundant in the samples and will be dealt with most fully.

A straight line relationship means that K or "condition" values calculated from the formula $K = 100W/L^3$ (where W is the weight of the fish (g.), and L its length (cm.)), may be directly compared between different size-groups. To calculate the K values, the material for each month was initially grouped in 5 cm. size-groups: e.g. the 30 cm. group refers to fish of 30-34 cm. In each sample, the mean length of each size-group was calculated together with its mean weight (g.), and the K value calculated therefrom. To obtain a reasonably regular 12-month cycle of K values, the three most abundant size-groups of each sex, and the three years 1946 to 1949, were combined by averaging the *K* values and plotting these averages in Figures 6 and 7. Preliminary plotting had shown little consistent difference in the level of the *K* values between years, while averaging the values of the different size-groups is justified from Figure 5*B*. Only the 35, 40, and 45 cm. groups were used in the females and the 30, 35, and 40 cm. groups in the males. These size-groups do not include immature fish.

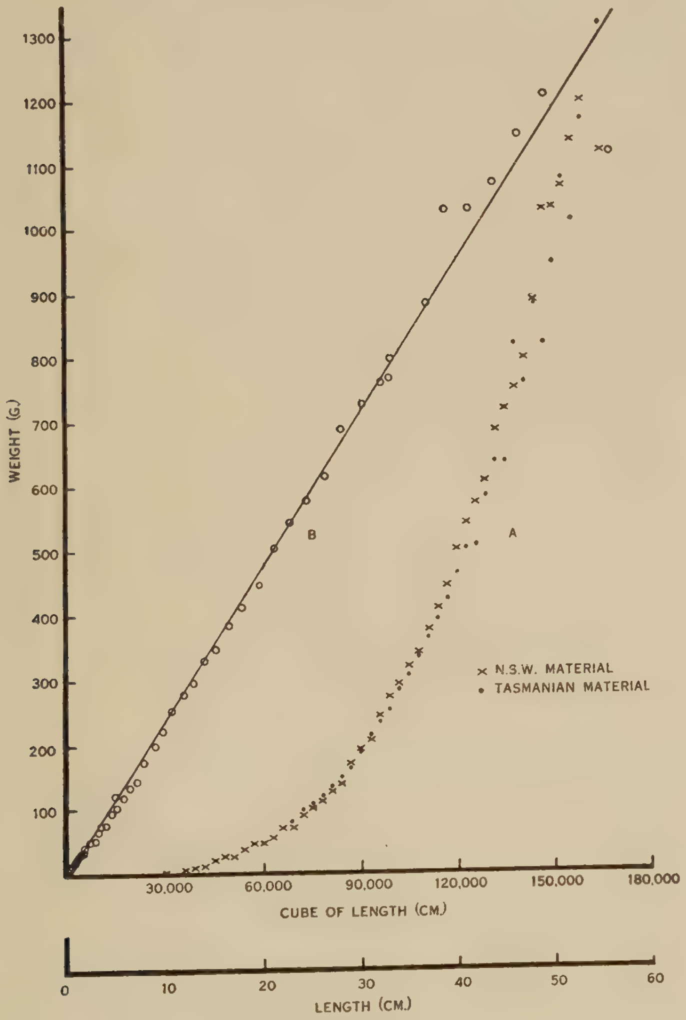

Fig. 5.—The weight/length relationship in the flathead. *A*, the average weight of each cm.-group plotted against fish length; the New South Wales market material has been augmented below 30 cm. with samples obtained by experimental trawling using a covered codend. *B*, the New South Wales material plotted as weight against the cube of the length, and a straight line fitted by eye.

The irregularities in the individual monthly *K* values are due in some cases to small sample size, but are largely a result of the random nature of the sampling. It was impossible to obtain a good continuous series from any one locality, and as a result, samples of fish in widely different stages of gonad development are often liable to occur in the one month. The average *K* values of the whole and gutted female flathead are plotted in Figure 6.

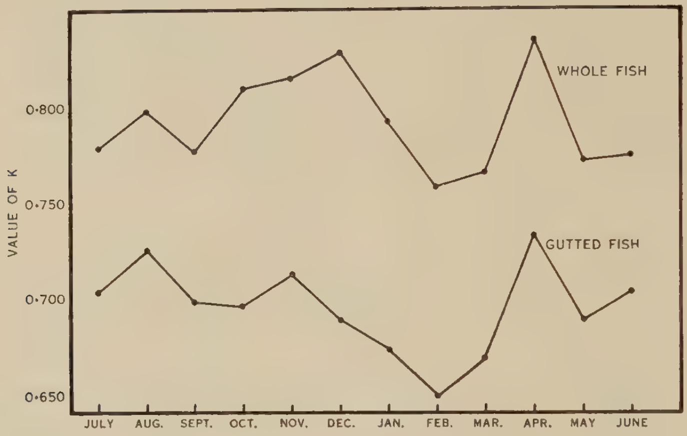

Fig. 6.—Condition factor (*K*) in the female flathead. Mean monthly values of *K* (May 1946 to May 1949) of the 35, 40, and 45 cm. size-groups.

While discussing Figures 6 and 7 it will be as well to refer to the rather fuller (but less extensive) results of the early years for confirmation of the general trend of the *K* values. Average values, corresponding to those plotted in Figure 6, are therefore given for the years 1941-42.

Taking the whole fish in Figure 6 first, it is evident that the fish are getting heavier during the spring, with high values in the summer. Actually, the graphed figures show a maximum in December, while the figures for 1941-42 show a maximum in September. Both sets of figures then show a fall in late summer to a minimum value in February or March. The more mixed origin of the graphed values is apparently having a "damping" effect, as might be expected, on the amplitude of the fluctuations. In April there is a rather surprising peak, which will be referred to later.

The gutted fish show a fall in *K* values from early spring to a well-marked minimum in February. After that there is a rise to a peak in April corresponding with that for the whole fish, and then a fall. In the flathead there are only small deposits of mesenterial fat and neither these nor the liver show any marked seasonal changes. The gutted fish weights may therefore be expected to reflect the drain by the gonads on the soma, and this is evidently what Figure 6 shows. *K* values are high in the late winter and early spring, when the gonads are recovering. As the gonads rapidly enlarge during the summer (see also Fig. 3) "condition" falls off. It reaches a minimum coinciding with the month of minimum weights of the whole fish—that is, after spawning has finished in the individual, though not necessarily in the population. The two lines in Figure 6 converge in winter and diverge in summer, the divergence being due to the enlarging gonads.

The secondary peak of both gutted and whole fish in April is surprising. It is marked in each individual year and also in the 1938 material. Moreover, reference to the original data sheets shows that the fish were mostly in the "recovering" stage, so that the effect cannot be due to the presence of late-spawning fish. It seems that growth and environment at this time of the year produce a state conducive to high "condition" values; which apparently does not persist, for the "condition" quickly falls off. It is suggestive that there should be an apparent tendency to form supernumerary annuli in the otolith at about this time of the year (Fig. 12).

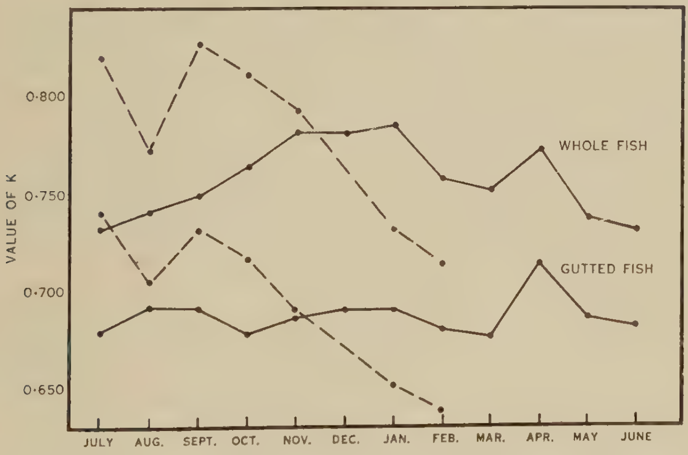

Fig. 7.—Condition factor (K) in the male flathead. Mean monthly values of K (May 1946 to May 1949) of the 30, 35, and 40 cm. size-groups. Some additional values obtained in 1941-42 are indicated by the broken lines.

Figure 7 treats the male flathead similarly, but in this case the values from 1941-42 have also been drawn in (broken lines). Evidently, in the gutted fish, the fluctuations have tended to cancel one another out; and if we are to say that there is a minimum in February or March corresponding to that of the female fish, it must be from the evidence of the 1941-42 material, which certainly suggests a minimum at about that time. The whole fish, however, do show the high summer values one would expect. Again, there is the peak in April shown also by the 1938 material.

Summarizing, in the female the flesh shows high "condition" values in winter and spring; these fall during the summer with the ripening of the gonads and reach a minimum probably as spawning ends; from this point they again begin to rise. The males probably show much the same cycle, with a minimum at the same time of year, but the changes are less marked. Comparison of Figure 6 with Figure 12 suggests a correlation between periods of translucent growth by the otolith with periods of high *K* values.

(*c*) *Populations of the Flathead and the Catch by Areas*

The presence of more or less genetically distinct populations can reasonably be discounted. The species occurs continuously between its geographic limits, and spawning takes place at many points throughout this range. The eggs and larvae are pelagic, and could hardly fail to be well distributed by the currents and counter-currents that sweep the east Australian coast at an average of 1-3 knots. In fact, platycephalid larvae of several species, but almost certainly including *macrodon*, have been taken in numbers over the whole continental shelf, and some of the richest hauls have been made 15 miles out to sea. Experimental trawling using a covered codend has shown that O-, I-, and II-group flathead occur in numbers all along the coast from Eden to Newcastle. Moreover, the known habits of the species are constant throughout its range, and spawning, in particular, shows a continuous seasonal progression.

It has so far been impossible to distinguish any morphological differences (proportional measurements, fin ray counts, etc.) between flathead from different parts of the coast. Specimens have been examined ranging from southern Tasmania to Newcastle, N.S.W.

However, a study of the growth rate shows that there are slight differences between samples from northern and southern areas (Section III (*c*) (ii)). Moreover, the otoliths of the younger age-groups from the Newcastle area have distinctly clearer markings than those from Ulladulla and southwards (Plate 3). The samples of older fish from the northern localities do not show the phenomenon so clearly, and it seems that they are being "diluted" by an influx of fish with poorly marked otoliths.

From this it appears that the young fish of up to two and three years old do not travel widely. It seems that, after the young fish have reached sexual maturity and moved out into water deeper than 35 fathoms, there is a certain amount of "wandering" which distributes them along the coast. It is probable that the young fish remain very much in the one place. Amongst the two-year-olds it is usual to find that fish from the one haul all have otoliths with very similar markings. During the experimental trawling a haul was made off Jervis Bay that took two-year fish with very distinctive otoliths; another haul at Wreck Bay, not more than 20 miles distant, took fish with recognizably different otoliths; on two subsequent monthly visits the fish with distinctive otoliths were found off

Jervis Bay. This uniformity of otoliths from the one sample begins to be lost in the III-group and older fish.

Turning now to Figure 8, we can compare the length frequencies of the flathead in each area to determine whether these also indicate a continuous and uniform population. Figure 8 has been constructed after the manner of Sund (1930). The annual length frequency curve of each locality in each of two biological years (1946-47 and 1947-48) was drawn up from the market measurements, and this was "weighted" according to the catch of flathead in that year at that locality. From these weighted curves a total, or "average" length frequency curve was calculated for the two years combined. Percentages were then calculated for the locality and the total length frequency curves and the difference (plus or minus) at each size-group of the percentage locality curve from the percentage

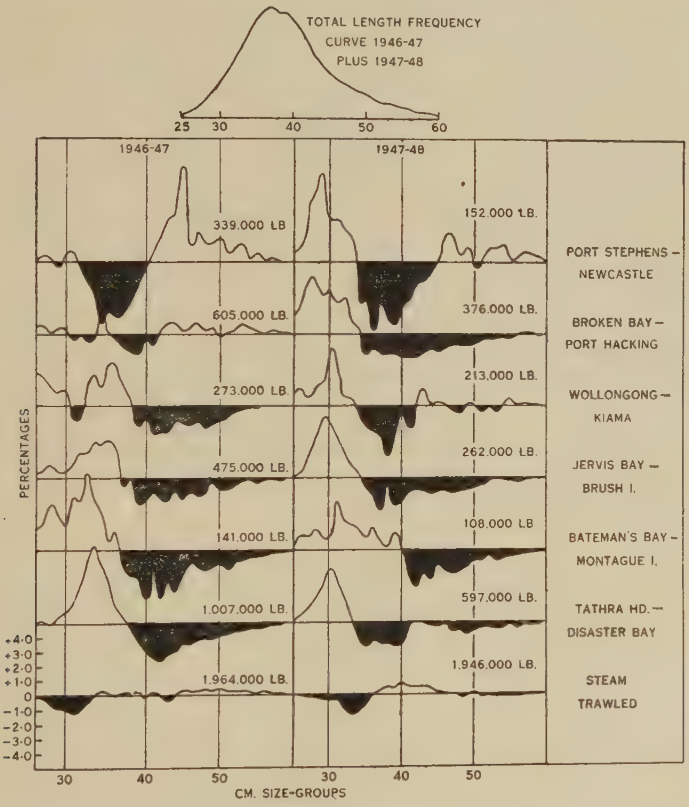

Fig. 8.—Differences (negative shaded, positive white) of the percentage length frequency curves of flathead from different localities from the mean percentage length frequency curve. Localities arranged in order from north to south. The origin of the steam-trawled flathead is not known but can be assumed to be off Eden and in eastern Bass Strait. The catch (lb.) at each locality is indicated.

total curve was calculated. These are plotted in Figure 8, the negative part of each curve being shaded and the positive left white.

This rather complicated treatment makes comparison between the curves simple. Taking the year 1946-47 first, but ignoring the curve for the steam trawler catch, it is evident that the population of the four southernmost localities exhibited an excess of small fish of up to about 38 cm. in length, and a deficiency of large fish. In the northern locality (Newcastle) the reverse held true and the fish from off Sydney were intermediate in this respect. There is no great difference between the curves in 1947-48, save that for Bateman's Bay-Montague Island, which can be discounted on the grounds of inadequate sampling. The Newcastle samples again show an excess of large fish. The steam-trawled samples show an excess of large fish in both years, and a deficiency of small; the most likely explanation of this is that the larger gear of the steam trawlers tends consistently to take larger fish than does the Danish seine.

It is evident that, though there may be slight differences in the length frequencies of the flathead population from one area to another, these differences are not great, save at the northern limit of the fishery, and are certainly not abrupt. This is a matter of some importance to the sampling technique, but also concerns the present argument in confirming the uniform nature of the flathead population and the absence of definable subdivisions.

The presence of more than one natural centre of distribution would suggest the presence of more than one population. Table 6 gives the catch and rate of catch of the main fishing centres in three years. The natural supply of flathead in each locality was being seriously affected, at least in 1946-47 and 1947-48, by the incidence of fishing. Danish seiners fish most heavily those areas which provide a good natural supply of fish, and have convenient marketing facilities. The table shows that the rate of catch in certain areas, such as off Sydney and Ulladulla, which are convenient for handling the catch, has fallen very suddenly compared with a distant locality such as Eden.

There are thus several confusing factors. In general, the total catch figures indicate concentrations of the flathead, while the rates of catch in the three years indicate the varying degree to which these concentrations have stood up to the fishing. The rates of catch of the Danish seiners have been adjusted to render them roughly comparable with the rate of catch by the steam trawlers (Fairbridge 1948, p. 92). It can be presumed that from 1947 onwards the trawlers' activities were confined to the area off Eden and southwards.

The greatest production is in the Eden, Ulladulla, and Sydney areas. The much lower rate of catch off Sydney in the later years shows that the natural population here is not as large as at either of the other two, while the far higher production off Eden shows a naturally greater production here than off Ulladulla. The low rate of catch of the steam trawlers shows that the available quantities fall off to the south of Eden; while the flathead population of south-east Tasmania is certainly not to be compared wtih the average of the New South Wales trawling grounds (see Blackburn and Fairbridge 1946).

The Eden area thus appears to be a single centre of distribution, with the quantities of available flathead falling off to north and south. This area is, in fact, at about the geographic centre of the flathead's range. In this area, too, the experimental trawling consistently produced the richest hauls of O- and I-group flathead.

TABLE 6

TOTAL CATCH AND RATE OF CATCH IN CHIEF FISHING AREAS

	1945-46			1946-47			1947-48		
	Catch (1000 lb.)	Rate of Catch*	Average No. of Boats	Catch (1000 lb.)	Rate of Catch*	Average No. of Boats	Catch (1000 lb.)	Rate of Catch*	Average No. of Boats
Port Stephens-Newcastle	124	140	3	339	90	8	151	36	10
Broken Bay-Port Hacking	830	687	4	605	87	18	376	61	18
Wollongong-Kiama	280	336	3	273	175	4	213	126	5
Jervis Bay-Brush I.	1,251	511	7	475	148	8	262	104	7
Bateman's Bay-Montague I.	126	100	7	141	129	4	108	88	4
Tathra Head-Disaster Bay	1,481	216	18	1,007	160	17	597	118	10
Steam trawlers	1,229	90	4	1,964	73	6-11	1,946	61	13

* Trawler-ton-months (Fairbridge 1948).

This pattern of distribution of the stock of available flathead supports the contention that there is a single population on the coast. Since the Danish seiners are dependent mainly on the III-group, the fact that local areas, such as that off Ulladulla, have become relatively depleted confirms that the younger age-groups do not make large-scale coastwise migrations. Probably tagging would be necessary finally to determine this point. Some tagging was carried out in 1944, and though there were a number of recoveries up to two months after the experiment, the technique was considered to be unsatisfactory.

(*d*) *Seasonal Catch*

Figure 9 illustrates the seasonal catch of the flathead in each area of the fishery. The points represent the mean rates of catch (catch per unit effort) for the years 1945-46, 1946-47, and 1947-48. Again, no information is available as to the area in which the steam trawler catches were made, but it is safe to assume that the bulk were in the area off Eden and southwards; the trawler polygon is therefore placed at the bottom of Figure 9, so that the areas run from north (top) to south (bottom).

There is a well-marked seasonal pattern. The most important localities (see also Table 6) are Broken Bay-Port Hacking, Jervis Bay-Brush Island, and Tathra Head-Disaster Bay, together with the trawlers. It is clear from consideration of the spawning cycle of the flathead (Section II (*a*) (ii)) that the major mode in each of these cases corresponds with the season of maximum spawning in the area, which is earlier in the north, beginning in October, and ceases in the south about March or April. The minor mode in October of the Jervis Bay-Brush Island line is consistently indicated in each of the three years, and it is significant that the earliest reports of spawning flathead usually come from this area. The less important localities are all intermediate between the major localities. The major mode of each line evidently corresponds with the season of spawning of the flathead in that particular locality. At this time the individuals tend to bunch together more in shoals, and become a relatively easy mark for the fisherman.

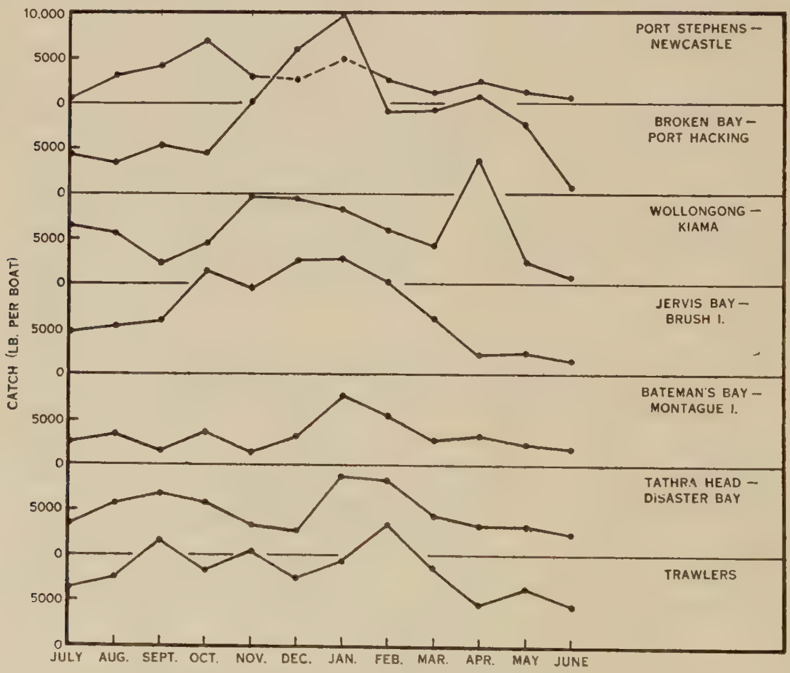

Fig. 9.—Seasonal distribution of the flathead catch; rate of catch by months and areas. Danish seiners' catches expressed in lb. per boat; trawlers' catches expressed in lb. per trawler-ton.

(*e*) *Food and Feeding*

Colefax (1938) treats the food and feeding of the flathead qualitatively and at some length. His material consisted of 657 stomachs collected throughout a year. In the present investigation an examination was made of about 2000 stomachs derived from the Sydney Fishmarket over the period 1946-48, together with about 1000 stomachs from earlier years taken in Tasmanian waters and some samples from small flathead collected experimentally. Somewhat more than half of these stomachs contained food remains.

A large proportion of flathead disgorge their stomach contents when brought to the surface. Hickling (1927) states that the habit of disgorging the stomach contents is, in the hake, correlated with the condition of the fish and also with the depth from which it is trawled. This makes any work on the season of maximum or minimum feeding of doubtful validity. Nevertheless, the gross volumes of the stomach contents of the Sydney Fishmarket flathead samples of 1947 and 1948 were determined on the chance of showing up any pronounced non-feeding season. The results show that flathead that have obviously been feeding heavily may be found in almost any month, so that it may be concluded that flathead feed whenever food offers. This may partly explain the irregular formation of annuli in the otolith.

Colefax (1938) points to the form of the flathead, its dorso-ventrally flattened head and body, the undershot jaw, the large, raptorial canines, and the upwardly directed eyes. Obviously the flathead does not look to the bottom for its food, though it may spend a considerable time resting on the bottom. Colefax suggests that the flathead is largely a mid-water feeder. Since the experimental hauls were made in the present investigations with an otter trawl fitted with covered codend, the ecology of potential forage species has become better known. Many of the species thought by Colefax to be mid-water feeders may be taken within a few feet of the bottom, often in large numbers. *Apogonops anomalus* has been taken in the trawl at the rate of five or more baskets in an hour's shot. Similarly, *Argentina elongata*, young cucumber fish, young nannygai, and bellows fish are taken in the trawl, and even the young of such an obviously pelagic type as *Trachurus*. It is likely that there is also at times a large population of Euphausiacea close to the bottom (compare for example, Wiborg 1948). The question of whether or not the flathead is a mid-water feeder must therefore be left in abeyance, since it could evidently make up its known diet from the water within a fathom or two of the bottom. On the other hand, the work using a covered codend confirms that the flathead does not feed directly on the bottom. The diet of other species shows that a large population of amphipods and polychaete worms occurs in the flathead's environment; but the flathead does not avail itself of these types. Heterosomata (*Lophonectes*) also occur in very large numbers over all the flathead grounds, but are rarely taken by the flathead.

The composition of the flathead diet as shown by the present work is shown graphically in Figure 10. The New South Wales specimens have again been divided into those above and below 35 cm. The height of the histograms is drawn according to the percentage of stomachs (excluding empty stomachs) in which the particular organism occurred. Size of the organisms is not indicated; so that the *Macrura* and *Munida* histograms exaggerate their importance, and the significance of the eel, *Congermuraena,* is understated.

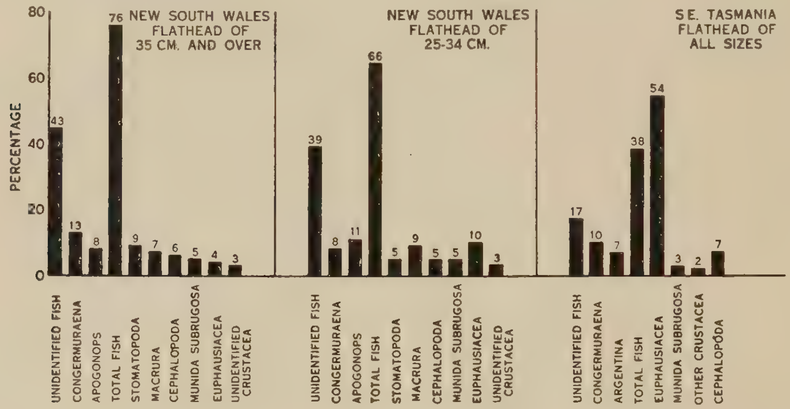

Fig. 10.—The food of the flathead. The number of stomachs containing a particular organism, expressed as a percentage of the total number of stomachs in which food was found. Fish species found in less than 5 per cent. of stomachs are not shown separately.

Fish species that occurred in the New South Wales samples but in less than 5 per cent. of the stomachs were, in approximate order of importance: *Trachurus* sp., *Argentina elongata, Chlorophthalmus nigripinnis* (the cucumber fish), *Macrorhamphosus* sp. (the bellow fish), *Lophonectes gallus, Trachichthodes affinis* (the nannygai), various triglids (gurnards), and a platycephalid. The histogram of Cephalopoda includes representatives of the squids, cuttlefish, and octopods.

Comparison of Figure 10 with Colefax's (1938) Figures 1-5 shows general agreement; but in the years covered by the present work, the Euphausiacea were of considerably less importance, with a consequent emphasis on the fish species as food organisms; while, among the fish, *Apogonops* was of less importance than Colefax found. The discrepancies found with Colefax's (1934) earlier work are probably real, and reflect changes in abundance of flathead, *Apogonops,* and Euphausiacea of the area. *Apogonops* was certainly commoner in stomachs taken during the latter half of 1946 and throughout 1947 than in 1948—a result in agreement with the experimental hauls. There seemed little seasonal variation in the occurrences of *Apogonops* and *Congermuraena,* the Euphausiacea showed a markedly higher occurrence in spring (August to October) while *Munida* showed a maximum in autumn (January to June).

About 75 stomachs of flathead below 20 cm. length were examined and less than half contained food. Down to a size of about 15 cm. there was no remarkable difference in diet; the fish species were smaller on the whole, and *Congermuraena* was not taken. Below this size there was a marked predominance of Euphausiacea in the diet; however, most of these samples were obtained in the spring, and the predominance of Euphausiacea may have been seasonal.

The Tasmanian material was collected in 1944 and 1945. Of those examined, 480 contained food, and the chief organisms are shown in Figure 10. The average size of the flathead was very much the same as in the New South Wales market samples. However, there are differences in diet. There was a greater emphasis on the Euphausiacea, which are by far the most commonly occurring organisms, in large as well as small specimens, and occurred more or less uniformly throughout the year. *Congermuraena* occurred in about the same proportion as in the New South Wales samples, but apparently *Apogonops* does not occur in south-east Tasmanian waters and *Argentina* takes the place of this species in the diet of the flathead. There were no Stomatopoda in the Tasmanian samples. Other fishes were the common Tasmanian species that one would expect to occur—gobiids, young *Thyrsites atun* (Euphrasen) (barracouta), *Clupea bassensis* (McCulloch) (sprat), young *Emmelichthys nitidus* (Richardson) (pearl fish), *Coelorhynchus* sp. (whiptail), young *Physiculus* sp. (cod), young *Dactylopagrus macropterus* (Bloch and Schneider) (perch), and triglids. As in New South Wales, there seemed no season of the year when feeding was markedly slacker.

Summarizing this section, it is evident that the flathead is a species that actively seeks its food at all times of the year, is a very catholic feeder and will take almost anything offering that swims off the bottom. *Lophonectes gallus* (Günther) (a small flatfish which is uniformly common on the New South Wales trawling grounds) is rarely taken, and even the small flathead apparently do not feed upon the quantities of bottom-living Cumacea, ostracods, *Munida*, Brachyura, and brittle stars found in the stomachs of the gurnards, *Lophonectes*, and jackass fish living on the same grounds. The flathead looks upwards for its food, and species remaining on the bottom are safe from it. On the New South Wales grounds, small fish provide the bulk of the diet, but Euphausiacea are of great indirect importance as food for the small fish on which flathead feed. The flathead is probably not a mid-water feeder, but is indirectly dependent on the bottom as a source of food supply for many of its small forage species.

III. Age Determination by means of the Otoliths

(*a*) *First Considerations*

Dakin (1939) formed the opinion that it was possible to use the otoliths of the flathead to determine their age, but made no critical examination of the method. His photographs show that the otolith annuli are not the unequivocal markings they are in the plaice, as evidenced by the photographs published in Wallace (1907).

(i) *Technique of Collecting and Handling the Otoliths.*—Scales are sometimes preferred to otoliths because of the ease of collection. In the flathead, it is possible to extract otoliths from 150 fish in three-quarters of an hour. Collection is therefore no difficulty. The otoliths are extracted with the fish lying on its back; the buccal cavity is entered through the gill opening, the skin removed from above the otic cavity with a penknife, the top (actually the ventral surface) of the otic cavity, comprising portions of the synpterygoid, pro-otic, and basioccipital bones (see Kesteven 1926) is sliced off, and the point of the knife is then jabbed into the side of the otic cavity and twisted so that the otolith of that side projects upward (ventrally) and may be removed with forceps.

A modification of the otolith board devised by Blegvad (1927) was used. This and the celluloid strip method of measuring lengths obviated any use of paper and facilitated single-handed work in the fish market, or at sea. The otoliths were stored after removal from the otolith board in small envelopes numbered according to the length-group of the fish.

In the laboratory the otoliths were read by immersing them in water in a black dish. Twenty or so otoliths were placed in a dish so that many specimens of one sample could be viewed simultaneously and compared directly. If left in water for more than an hour the otoliths became translucent but this proved to be no advantage. Several clearing agents, xylol, and clove oil, were tried but were found unsatisfactory.

It is difficult to understand why Dakin (1939) ground his flathead otoliths; his photographs do not show this laborious process to have any advantage over the examination of whole otoliths; rather, the reverse is true. Grinding was therefore not used in this investigation.

Following the method used by Hickling (1933), the otoliths were examined by direct light through a low-power dissecting microscope (about 3.4×) fitted with a micrometer eyepiece. Transmitted light and higher magnification merely obscured the overall pattern.

(ii) *The Otolith and the Method of Reading.*—Plate 2, Figure 5, shows the orientation of the otolith. Plate 2, Figure 6, shows the otolith as it would be seen from above, lying in the otic cavity. It is bent like a boomerang, with the bend slightly behind the mid point, and the outer surface of the two halves more or less straight. The angle of bend is variable, as is the general form of the otolith. Fissures run upwards from the central portion and give the dorsal edge a scalloped outline; the degree of fissuration is very variable, but tends to be less in the older fish. The otolith of this species is always clearly distinguishable from that of *longispinus* (Macleay) and *speculator* (Klunzinger) (= *grandis* Castlenau = *conatus* Waite and McCulloch), the only two species liable to be confused with it in the field.

In *macrodon* the two otoliths from one fish are virtually identical in general form and in the pattern of growth rings. Occasionally one of a pair is "crystallized" (in this condition the organic matter is in part or whole either not developed or has been resorbed, leaving a mass of large calcite crystals) ; these otoliths are usually useless for age determination, and when possible they are discarded in the field and the otolith from the other side is taken. Rarely both otoliths are more or less "crystallized".

The method of age determination from the growth rings of otoliths has been fully discussed in fisheries literature. Molander (1947) and Gross (1947) have demonstrated critically the validity of the assumption that the opaque bands of the otolith represent the periods of relatively fast growth and the semi-translucent bands the periods of slower growth. Hickling (1931) has discussed in detail the microscopic structure of the otolith.

Seen in good light, under water, and against an opaque, black background, the alternate bands of opaque and semi-translucent material may be seen readily with the naked eye. Under the low-power microscope a central nucleus is clearly defined in most flathead otoliths, and absent in very few. It is difficult to photograph flathead otoliths in such a way as to show up all the features at the same time; the nucleus can best be made out in two of the small otoliths of Plate 3, Figure 4. It is evident that this nucleus is the centre around which growth began, and from which growth has proceeded in all directions but at different speeds in the different planes. It is a useful datum point for growth measurements.

In an otolith the annulus is a *band* of translucent material, not a sharp break or line as in the scales of some species. In the flathead otolith there is not usually much doubt as to the darkest (most translucent) central part of the translucent band, and readings are therefore made to this point. Where there is serious doubt, as in the second annulus of Plate 2, Figure 4, the reading is omitted. Where no nucleus can be made out, its position can be estimated with fair accuracy. Intermediate lengths are measured, with the eyepiece micrometer, from the nucleus to each annulus along a line from the nucleus to the most anterior point of the otolith (*a* in Plate 2, Fig. 5).

(iii) *Proportional Growth of the Otolith.*—A review of the literature shows that, while the technique of age determination from the otoliths is well established, the calculation of intermediate lengths from the otoliths has seldom been attempted. Apparently either little need has arisen, or the form of the otoliths has been unsuitable, or as Jensen (1938) found for the plaice and the dab, fish and otolith grow disproportionately, and the degree of disproportion may vary from place to place.

Hickling (1933), however, being unable to capture O-group hake, used the technique of back-calculation from the intermediate lengths of the otoliths to calculate the growth in the first year. He found that above a fish-length of 32 cm. there was a straight line relationship between growth of otolith and fish, but below this the line curved towards the fish-length axis. No otoliths were available to him from fish of less than 14 cm. He extrapolates the line from this point (a fish-length of 14 cm.)

and finds that it cuts the fish-length axis at about 5.5 cm. He comments: "It would appear, therefore, that the sagitta is formed when the fish is about 5.5 cm. long." This raises the question of the identity of those bodies usually referred to as otoliths in the very young fish larva (e.g. Regan 1916; Ehrenbaum 1909) and also the question of the function of the otolith—if it is suggested that the fish lives to a length of 5.5 cm. without an otolith. Actually there seems little justification for extrapolating the fish-length/otolith-length curve in this manner, for there may well be more than one change in the relative growth of the otolith below a fish-length of 32 cm.

More recently Zamakhaev (1941) worked on the measurement of intermediate lengths in cod otoliths, and calculations of the intermediate fish-lengths. The value of this paper is severely limited by his omitting to demonstrate whether or not there is proportionate growth of the otolith.

The necessity of demonstrating proportionate growth, or of making allowance where growth is disproportionate, has of course been widely recognized in work on scales. There the problem is complicated by the fact that scales are not developed until a fish is a few centimetres long, that they do not all develop simultaneously, and that their subsequent growth in proportion to the fish is different in different parts of the body. To some extent, therefore, the use of otoliths is simpler.

In the flathead, growth has been found to be proportionate down to a fish-length of 10 cm. Considerable use has therefore been made of intermediate lengths. The markings of the flathead otolith are most clearly read in the dorso-posterior sector. Intermediate measurements might be accurately made along either the lines *a* or *b* in Plate 2, Figure 5. These two measurements were made on a series of samples, taking particular care to keep the magnification constant.

Length measurements (line *a* in Plate 2) were taken from 1,027 samples of otoliths from the area Newcastle to Port Hacking, 825 samples from Tathra Head to Disaster Bay, and 498 samples from south-east Tasmania. These samples represent the centre and extremes of the flathead range. In each case the distribution approximates very closely to a straight line. This is particularly true of the most numerous, Port Hacking to Newcastle data. The material includes the largest sizes of flathead taken. Though the mean values here are more irregular, they show no consistent divergence from the straight line. The points for the smallest flathead, however, approach the fish-length axis. The regression lines were therefore calculated only for the flathead of 10 cm. and over.

It may be concluded that, above a fish-length of 10 cm., there is isauxetic growth of the otolith. If extrapolated, the regression lines would cut the fish-length axis at a negative otolith-length value; this is absurd, and presumably there is, in the very small flathead, disproportionately faster growth of the otolith, with values commencing at the origin in Figure 11.

A preliminary study of the otolith width (line *b* in Plate 2, Fig. 5), treated in the same manner, indicated that the relationship with fish-length was not as simple as the one just mentioned. This measurement was therefore not continued.

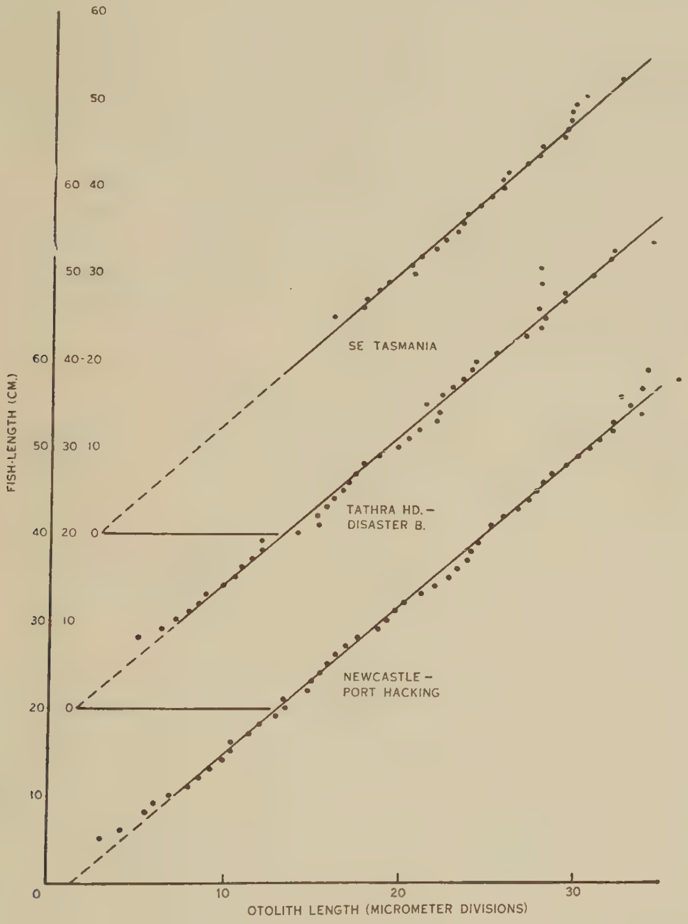

Fig. 11.—Regression of otolith- on fish-length for three localities. The points are the mean values for each fish-length unit. Values below 10 cm. fish-length are not included in the regression calculations.

The basic formula used in calculating the intermediate lengths may be written: $l = \frac{L}{V} \times v$, where l is the intermediate length, *L* the fish-length, *V* the total otolith length, and *v* the distance from nucleus to annulus. If, however, the regression line of otolith-length on fish-length does not pass through the origin, this proportionality will not hold and must be adjusted. In the present instance, a pooled regression line for the two New South Wales samples cuts the otolith-length axis at a value of approximately 1.5 micrometer divisions. By subtracting 1.5 from both V and v in the above formula, the proportionality is restored above a fish-length of 10 cm. This practice has therefore been adopted in calculating the intermediate lengths from the otolith readings. This adjustment lowers the l_1 reading in a V-group fish by about 2 cm. and the other intermediate lengths progressively less. Below a fish-length of 10 cm. it must be remembered that the technique is not altogether accurate.

(iv) *Season of Formation of the Annulus.*—The terms "translucent" and "opaque", referring to growth zones in the otolith, are not absolute; they acquire meaning partly by comparison one with another. This makes it difficult to identify translucent zones at the edge. Opaque zones at the edge stand out clearly enough; but where an opaque zone is merging into translucency, it is often impossible to tell whether the centre of the translucent zone has been laid down, unless further opaque growth on the edge has been formed.

TABLE 7

MONTHLY MEAN VALUES OF GROWTH INCREMENT BEYOND TRANSLUCENT ZONE OF I- AND II-GROUP FISH

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
I-group	10.9	11.4	8.8	9.5	1.0	4.0	1.9	1.9	7.3	6.4	—	7.1
II-group	6.3	5.6	3.9	8.2	2.6	3.6	3.1	3.4	3.1	3.5	4.4	5.4

This difficulty is largely overcome if the season when the majority of the fish lay down the translucent zone can be determined. A convenient date may then be chosen as the "arbitrary birthday" and the age of any specimen related to this. A special study was therefore made of the growing edge. Two methods were used.

The first method was limited to I- and II-group fish. Otoliths of these age-groups are generally very clear and not confused by supernumerary annuli. The samples containing these smaller fish were examined and the increment beyond the last indication of a translucent zone was measured, irrespective of whether or not that zone was suspected of being supernumerary. From this, the last growth increment of the fish was calculated by the usual method. All the material from New South Wales up to June 1948 was used, including samples from all parts of the coast. The mean values were calculated for each month, and are given in Table 7. The figures clearly indicate the rather sudden onset of annulus formation in May, with opaque growth beginning in August or September.

The material was not full enough to compare differences between years. There do not appear to be consistent differences between localities. An excellent series, covering the whole coast in each month, was obtained experimentally in October, November, and December of 1948; opaque growth in these samples had already begun by October, and the marginal zone was of approximately equal width in samples from all localities.

The second method for determining the season of formation of the annulus was designed to obtain an entirely objective estimate valid for the older fish. Two samples from each month of 1946 were selected, and each was taken at random and examined in ignorance of its date. The examination was made with the naked eye, simply recording whether the edge was opaque or translucent. The percentages of the 31-50 cm. fish with an opaque edge are shown graphically in Figure 12. Each month was represented by between 60 and 110 fish.

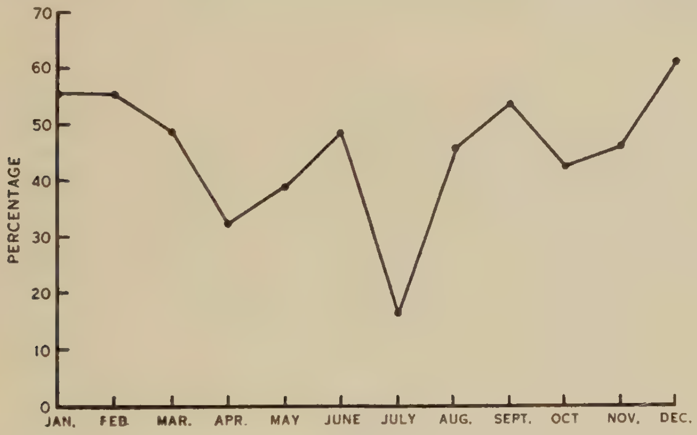

Fig. 12.—The seasonal incidence of otoliths from the older flathead with an opaque edge; percentages calculated from data drawn from two samples in each month of 1946.

The generally low percentage values should be noted, but there is a clear minimum in July. There is also an indication of the formation of a supernumerary annulus in April, which corresponds with a similar tendency noticed in the young flathead from Eden in 1946 and again in 1948.

In other species annulus formation is usually correlated with spawning or with the winter. Figure 13 illustrates the sea-water temperatures at 50 m. depth from four stations over the 25-30 fathom contour off the New South Wales coast. It is apparent that the months in which lowest temperatures occurred include August, September, and October — the months of onset of opaque growth in the otolith. In particular, some samples of young flathead taken in 25 fathoms off Eden in August 1947 all showed the completion of an annulus and the start of opaque growth, yet Figure 13 shows that the lowest temperatures occurred in the following month. While the annulus is evidently formed in winter, the relation between its formation and sea-water temperatures does not appear to be direct.

Attention may be drawn here to the somewhat erratic sea temperatures typical of the New South Wales coast. Cold water incursions are liable at almost any time of the year. It may be that such irregular conditions are indirectly related to irregularities in the formation of true and supernumerary annuli in the flathead otolith.

It is now possible to select a date, equivalent to what has been called the "arbitrary birthday", that will serve to divide sharply the age-groups. As this date is passed, each year-group of flathead is regarded as automatically passing into a higher age-group. The obvious date to choose is June 30, as new growth does not usually begin before this date. In this species it cannot be called a birthday, of course, since spawning takes place in summer.

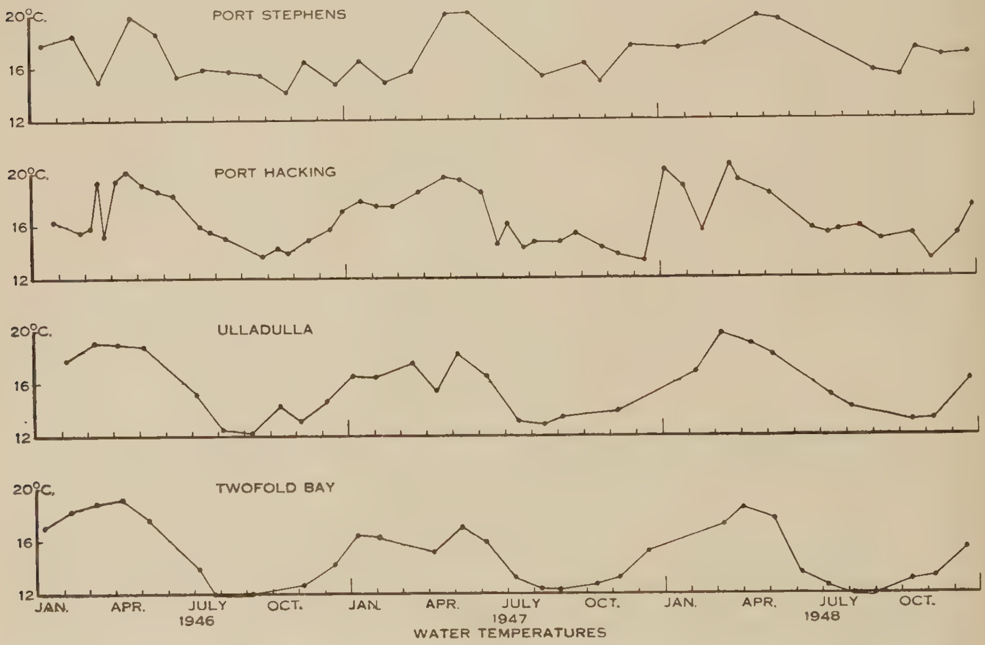

Fig. 13.—Mean monthly sea-water temperatures at 50 m. depth taken at four stations on the 25-30 fathom contour off the New South Wales coast. (Data supplied by the hydrology section of the Division of Fisheries.)

Following the usual practice, the age-groups in this paper are referred to as the O-, I-, II-group, etc.; the O-group refers to fish that have not yet passed June 30 (have no annulus in the otolith), the I-group are fish that have passed the date once (and presumably show one annulus), the II-group have passed the date twice and presumably show two annuli in the otolith, and so on. The O-group on June 30 are thus about 6-9 months old and the I-group on June 30 on the average about 18 months old. An otolith from a fish caught in June with one annulus well inside the edge and another on the edge would be classed in the I-group, and the outer annulus ignored for purposes of grouping it in its age-group; if there was a slight margin of new growth beyond this peripheral annulus, the annulus would be suspected of being supernumerary (cf. June values, Fig. 12), and after verifying that the fish-length agreed with the generally established range of I-group fish in June the specimen would again be classed in the I-group; if the margin of new growth were wide and the fish-length did not disagree with the range of the II-group, the specimen would be classed in the II-group in the belief that a winter annulus would yet be formed or (what is rare) had been omitted. The year-groups are designated by their summer of birth: thus, the III-group of 1947-48 would be assumed to have been spawned in the summer of 1944-45 and would be called the 1944-45 year-group.

(*b*) *Age Determination and Length Frequencies*

By comparing the flathead otoliths with published photographs of the otoliths of oversea fishes (e.g. plaice (Wallace 1907; Molander 1947; Gross 1947), halibut (Jespersen 1917), cod (Fridriksson *et al.* 1934), hake (Hickling 1933), Pacific pilchard (Walford and Mosher 1943)) it can be said that flathead otoliths are not good, though they are perhaps comparable in clarity with those of the hake and cod. As will be shown, they provide the best clue we have to the age composition of the flathead catch, and the results appear valid when tested in the various normal ways.

(i) *The Younger Age-groups.*—The otoliths of the I- and II-groups are usually clearly marked and afford little difficulty. These groups also can be readily checked against their length frequency modes. Apart from sporadic appearances in the fish market, the younger age-groups were obtained by experimental trawling using a cover of $\frac{3}{4}$ in. netting over the codend. These samples had the advantage of being free from net selection, save in the very smallest sizes of 9 cm. and under.

The length frequencies of the samples obtained experimentally are shown in Figure 14. Size-groups of 2 cm. have been used, and the summed values are plotted for each month from all localities. Figure 15 shows the length frequencies of the southern and northern samples treated separately. The months have been arranged irrespective of the year, in order to show the general progression of the modes. This treatment assumes that the length frequency distribution of the age-groups is more or less the same from year to year.

Knowing the season of spawning, it is easy to assign the major modes of June, July, and August 1947 (Fig. 14) to age-groups. There is evidently a mode between 10 and 15 cm., and another about 26 cm.; these must refer to the 1946-47 and 1945-46 year-groups respectively. The former represents about 6 months of growth and the latter about 18 months. Before these data became available, the intermediate lengths of the first and second annulus (arbitrarily assumed to be formed on June 30) had been back-calculated from otoliths of older fish, and found to be of the order of 9 and 21 cm.; the values obtained directly from the length frequency data were thus somewhat larger, but certainly of the same order. This was felt to be important confirmation of the method of back-calculation. The modes of these first two year-groups can be traced throughout the remainder of the length frequency curves in Figure 14.

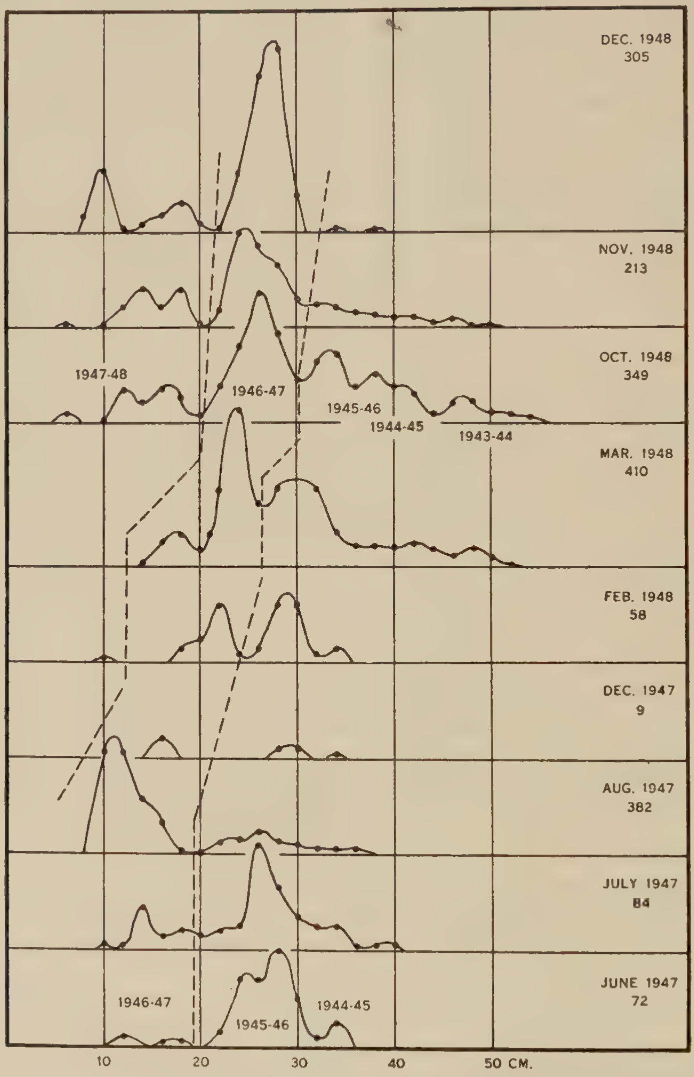

Fig. 14.—Length frequency curves of all the flathead obtained by experimental trawling using a fine-meshed codend cover. The major year-groups, verified by the otoliths, are approximately indicated by the broken lines. Size intervals of 2 cm. have been used and the curves drawn by eye. The number at the right of each curve gives the number of fish in the sample.

The 1946-47 year-group in March 1948 comprises a small mode preceding a major one, and the 1947-48 modes of October-December 1948 are each bimodal or even more complex. In these cases the simple length frequencies are not a sure guide to the age of the size-groups. The otoliths, however, effectively refer the modes to their year-groups, and these are indicated in the figure. The bimodality of the I-group is not unexpected, in view of the protracted spawning period. The small group at 6 and 8 cm. in October and November 1948 is difficult to interpret; it occurred in samples taken off Port Hacking where, in the following December, a large

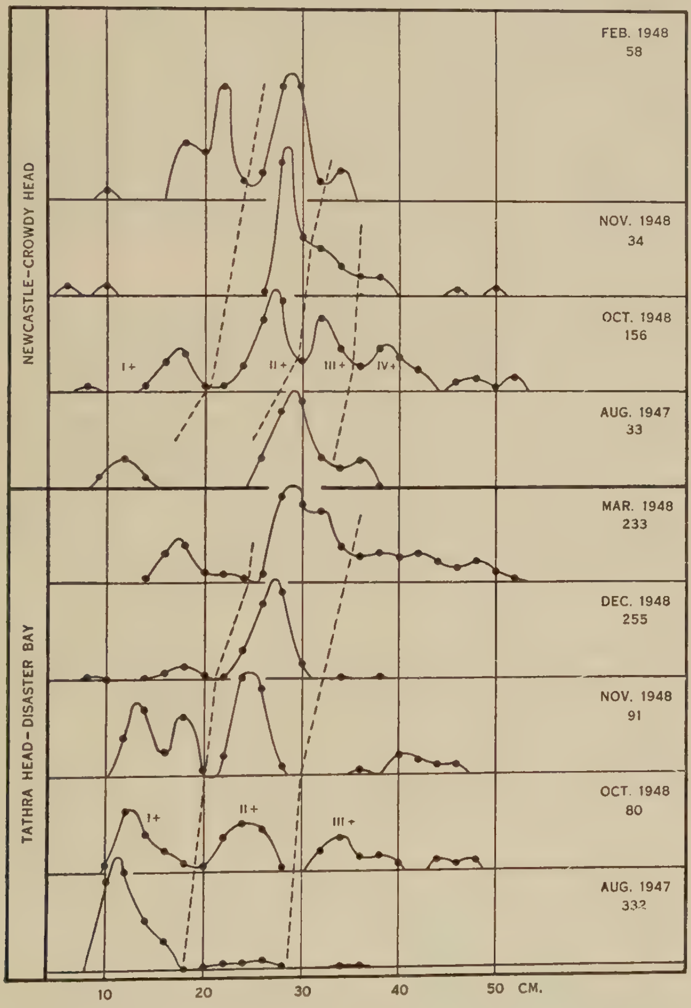

Fig. 15.—Length frequency curves of the flathead obtained by experimental trawling; samples from the southern and northern areas only, arranged according to the months, irrespective of the year. The age-groups are indicated as in Figure 14.

sample of small fish of 9 and 10 cm. (Fig. 14) was also taken—apparently representing the same batch, which had grown in the interval. Presumably they represent eggs spawned very late in the preceding autumn, and have grown to only 5 or 6 cm. by the following October. These fish had not laid down a clear first annulus.

The II-group mode is simpler by comparison with the I-group but tends to run into the III-group. The otoliths must always be used to distinguish the II-group from the III-group. The mode of the III-group can be clearly distinguished in some of the curves of Figures 14 and 15, but the IV-group mode is liable to be deceptive, particularly in small samples. In Figure 15 it will be seen that the modes of the first two age-groups in the northern samples fall at somewhat larger sizes than in the southern samples.

Reflecting the complexity of the I-group length frequency curves, the first growth zone of the otolith is sometimes confused. This may be seen in either the II-group or in otoliths from the older fish. Sometimes the first annulus is evidently missing; more often there are supernumerary annuli. It is common to find a very clear annulus between a calculated fish-length of 1 and 5 cm.; that is, very close to the nucleus. It is possible that in many specimens this represents the adoption of a bottom mode of life after their planktonic existence as larvae. Examples are shown in Plate 4, Figures 4, 5, and 6, where another well-marked annulus occurs in each not far outside this inner ring and is presumably a true winter annulus. Such inner annuli are provisionally referred to as larval annuli.

Of more difficulty are the occurrences of an annulus beyond the normal range of the first annulus. The wide spread of the I-group means that these cannot be ruled out as true winter annuli. Their validity must be decided by considering their position relative to the second annulus (which is usually the most clearly marked in an otolith), and by comparison with other specimens from the same sample. These difficulties are not serious in the early age-groups; where they do occur they can always be resolved by interpreting them from the length frequency groups. Experience with the early age-groups (because the results are independently verifiable) is most valuable in interpreting the otoliths of the older age-groups. The extreme clarity of the I- and II-group otoliths from the Newcastle area has already been referred to (Plate 3).

(ii) *Length Frequencies of the Market Samples.*—Two typical series of monthly length frequency curves from the market samples are presented in Figure 16. Clearly, they are of little direct use in age determination. When dissected according to locality, they become a little more useful. Figure 17 shows series from Eden, Sydney, and from the steam trawlers. The latter may be assumed to have been derived from localities south of Eden.

The first mode at about 30 cm. is apparent in most of the samples, and it can be seen to move from left to right. But this shift does not accurately reflect the growth of the age-group, since the left-hand side of the curve is being acted on by net selection. Flathead of up to the legal size (33 cm.) can escape through the meshes of the codend. It is evident

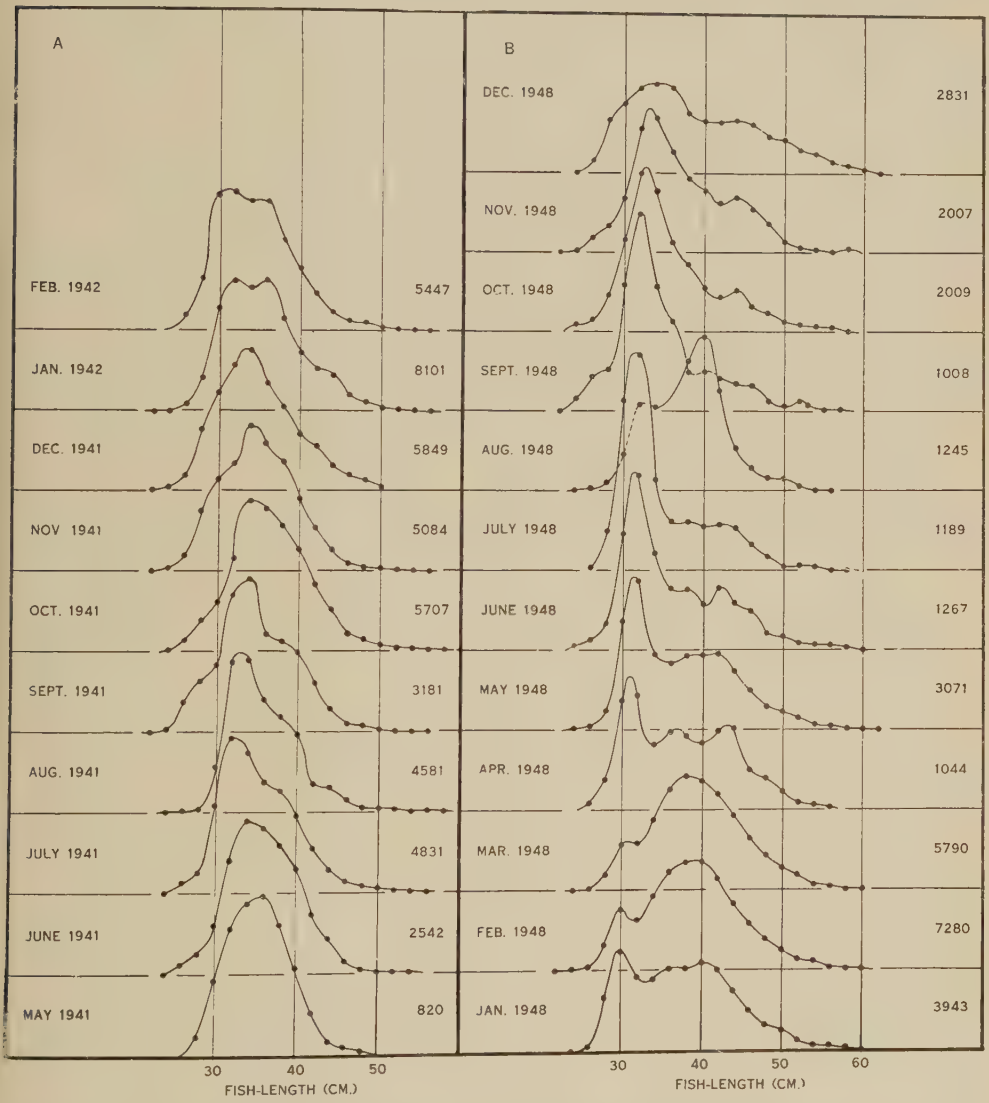

Fig. 16.—Two typical series of monthly length frequency curves; 2-cm. size-groups have been used, and the curves drawn by eye. The numbers making up the samples are indicated at right of each curve.

from Figures 16 and 17 that the capacity of the codend to retain flathead of less than 30 cm. falls off very rapidly, while flathead of 25 cm. are retained only on rare occasions.

After this first mode, it is difficult to choose the mode of a larger size-group and follow it through with any certainty. In the Eden series, a mode at 37 cm. in August 1947 may perhaps be identified with one at 42.5 cm. in June 1948, and this would be of the calculated order of growth for the IV-group (see later); but there is too much uncertainty to carry this line of reasoning further. For purposes of age determination, the length frequency curves of the market samples can only be used as an adjunct to the otolith method.

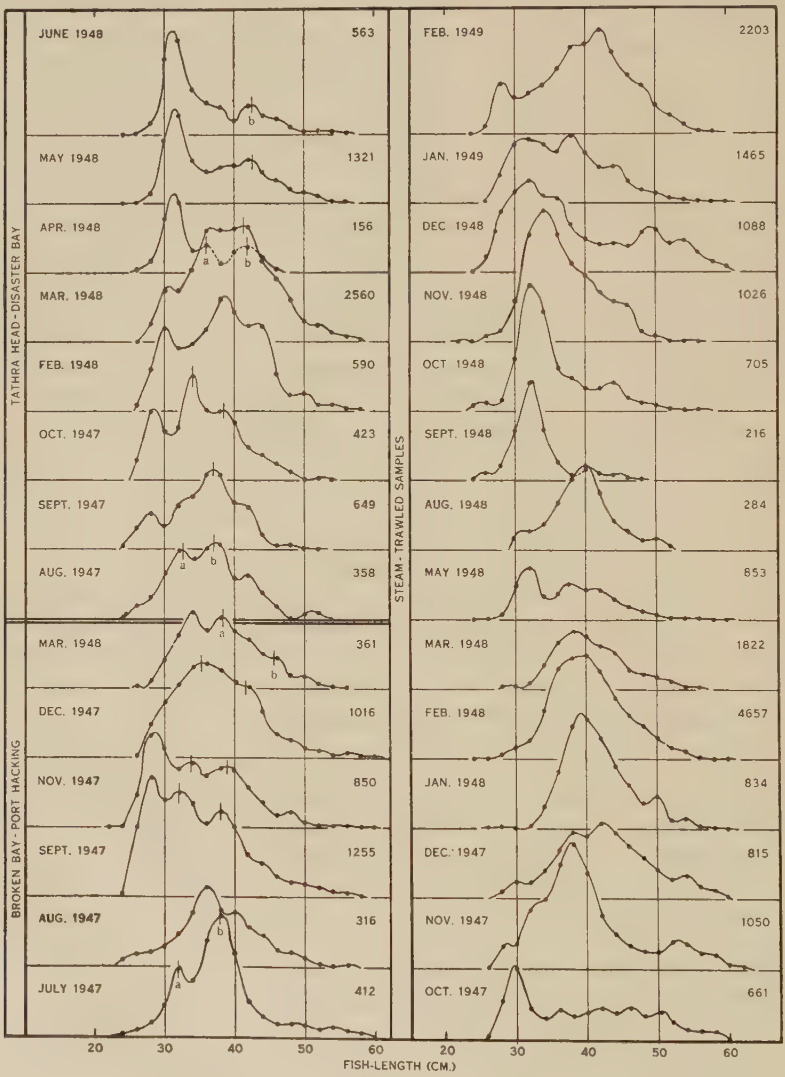

Fig. 17.—Three series of monthly length frequency curves. In the two left hand series suggested modes (*a* and *b*) are followed through. The numbers making up the samples are indicated at right of each curve.

(iii) *Age-groups in the Market Samples.*—Age determination from the otoliths of older flathead is very much less certain than for the younger age-groups. This is partly because little help may be had from the length frequency modes, but also because there is a marked increase in irregularity of the annuli.

In the first place, there appears to be an increase in the proportion of translucent material in the otolith, both in the form of supernumerary annuli (those formed at other times than winter) and also in the width of the annuli. Plate 3, Figures 4, 5, and 6, shows samples of typical I- and II-group otoliths; these are usually clear and indisputable (a good deal of the clarity is lost in the photographing). They may be compared with Plates 2 and 4, showing samples of otoliths from larger fish. It is possible that this change in the otolith may be associated with the onset of sexual maturity and spawning (cf. Rollefsen 1934).

Table 8 gives the gross results of the bulk of the age determinations. Each age-group has a very wide spread since samples have been drawn from every month of the year. Tables 9 and 10 show this material divided into localities.

TABLE 8

NUMBER OF FLATHEAD OF EACH CM.-GROUP ARRANGED IN AGE-GROUPS: 1946-47 AND 1947-48 AGE DETERMINATION DATA, INCLUDING THAT DERIVED FROM THE 1948-49 EXPERIMENTAL FISHING

Total Length (cm.-groups)	0+	I+	II+	III+	IV+	V+	VI+	VII+
5		2						
6		3						
7		—						
8		5						
9		24						
10	1	25						
11	1	23						
12	1	20						
13		23						
14		23						
15		31						
16	1	28						
17		42	1					
18	1	18	1					
19		4	1					
20		14	3					
21		15	10					
22		40	15					
23		50	41					
24		41	75					
25		25	150					
26		18	136	3				
27		8	206	8				

TABLE 8 (*Continued*)

Total Length (cm.-groups)	0+	I+	II+	III+	IV+	V+	VI+	VII+
28		13	172	13				
29		6	164	35				
30		2	109	41	1			
31			88	97	1			
32			70	141	5			
33			31	193	10			
34			20	164	33			
35			10	194	69			
36			2	177	101			
37			4	134	159	1		
38			3	123	189	5		
39			2	92	195	8		
40			2	79	201	17		
41				41	173	33	1	
42				25	183	29	—	
43				18	118	43	2	
44				8	98	44	2	
45				5	98	42	1	
46				3	66	51	1	
47					54	74	2	
48					35	46	5	
49					18	52	10	
50					15	50	3	
51					8	39	8	
52					2	33	10	
53					2	34	9	
54						17	17	1
55					1	4	20	1
56						7	7	3
57						—	7	1
58						2	8	2
59						1	5	1
60							1	—
61							1	—
62								1

After considerable experience, it was found that the author formed his judgment of true winter and supernumerary annuli on the following considerations: Firstly, the time of year at which the sample was obtained; this knowledge is essential in determining the validity of annuli close to the edge of the otolith. Secondly, the general symmetry or proportions of the growth increments; it is assumed that in the great majority of specimens the increments are not erratic, but decrease gradually with age. Thirdly, the actual values of the calculated intermediate lengths are borne in mind. This is done both unconsciously when reading the otolith (one comes to expect the micrometer readings of l_1, l_2, l_3, etc., to fall within certain limits) and also deliberately, after the intermediate fish-lengths have been calculated. The fourth and last consideration is the actual length of the specimen compared with the range of each age-group (Tables 9 and 10). The clear and indubitable otoliths of each sample are, of course, a useful guide in interpreting those with confused annuli; hence the advantage of setting out many otoliths (12-20) in the dish at one time.

TABLE 9

GROWTH RATE BY LOCALITIES; FROM MARKET SAMPLES, 1946-47

Locality		Age-groups					
		II+	III+	IV+	V+	VI+	VII+
		cm.	cm.	cm.	cm.	cm.	cm.
Broken Bay-Port Hacking	Range	27-34	32-43	34-52	43-55	48-58	52-58
	Mean	31.7	39.3	42.4	49.6	52.8	55
	No.	(6)	(109)	(173)	(97)	(18)	(2)
Wollongong-Kiama	Range	22-30	26-37	34-42	41-47		
	Mean	28.0	31.5	37.4	44.0		
	No.	(32)	(40)	(18)	(2)		
Jervis Bay-Brush I.	Range	28-34	26-41	33-45	37-52	44-54	
	Mean	31.0	34.3	39.8	44.9	52.0	
	No.	(9)	(94)	(102)	(29)	(9)	
Bateman's Bay-Montague I.	Range	27-38	30-43	34-50	39-53	49	
	Mean	30.0	36.1	43.1	46.8	49	
	No.	(5)	(79)	(41)	(36)	(1)	
Tathra Head-Disaster Bay	Range	25-35	29-42	33-45	38-58	41-53	56 -
	Mean	28.7	34.1	38.7	45.2	48.4	56.0
	No.	(24)	(163)	(189)	(57)	(5)	(1)
Samples from trawlers	Range	26-40	29-46	34-52	39-58	48-61	54-58
	Mean	31.6	36.4	42.4	48.7	54.9	56.2
	No.	(102)	(436)	(493)	(224)	(37)	(5)

Since the flathead spawns in summer, it is possible that the formation of supernumerary annuli is not altogether haphazard, but that there may be a definite tendency for each adult to form two annuli a year—one in winter and another at spawning time. Figure 12 does not show any evidence of this, but the author gained a subjective impression that many specimens do show some such regular alternation of winter and supernumerary annuli. Plate 4, Figure 4, shows such "doubling" well. Five annuli are clearly marked (one on the edge, with a suggestion of an opaque margin beyond) but midway between the second and third and between the third and fourth there are fainter, supernumerary annuli. Were all these annuli counted as true winter annuli, the specimen would be regarded as VII+, although only 46 cm. long.

Plate 4 illustrates some other otoliths that might be misleading. Plate 4, Figure 1, shows a clearly marked IV+ otolith with a supernumerary annulus (*s*) in the middle of the second opaque zone. Were this counted as an age mark, it would mean that the first growth zone (of only 3-9 months' duration) would be twice the size of the second and third. By regarding the annulus as supernumerary the first opaque zone is made about the same size as the second. On the average it is usually somewhat smaller (Table 11). Plate 4, Figure 2, illustrates a probable supernumerary annulus in the third opaque zone. This specimen was 31 cm. long in February, and according to the present interpretation would be turning IV+ on the following June 30; it would thus be somewhat small for its age. But if the annulus (*s*) were regarded as a true winter annulus, the specimen would be regarded as a year older and be highly aberrant in size-for-age. Plate 4, Figure 3, shows the rather uncommon case of a missing second annulus. The incompletely marked translucent zone just inside the l_3 is presumably supernumerary. Omission of the first annulus, as pointed out above, is more frequent. Instances of this may be seen in Plate 3, in the lower left specimen of Figure 5, and the lower right specimen of Figure 6.

TABLE 10

GROWTH RATE BY LOCALITIES; FROM MARKET SAMPLES, 1947-48

Locality		Age-groups						
		I+	II+	III+	IV+	V+	VI+	VII+
		cm.	cm.	cm.	cm.	cm.	cm.	cm.
Pt. Stephens-Newcastle	Range		35-37	33-41	37-48	46-53	55-59	62
	Mean		35.8	38.3	42.0	49.2	56.3	62.0
	No.		(4)	(11)	(20)	(5)	(3)	(1)
Broken Bay-Pt. Hacking	Range		23-32	29-37	35-47	42-54	54	53
	Mean		27.4	32.5	40.0	48.1	54.0	53.0
	No.		(199)	(13)	(23)	(12)	(1)	(1)
Wollongong-Kiama	Range	24-26	27-32	31				
	Mean	25.0	29.5	31.0				
	No.	(4)	(42)	(1)				
Jervis Bay-Brush I.	Range	22-25	24-35	28-40	34-50	38-47	45-55	
	Mean	23.8	29.3	34.2	39.5	42.5	50.4	
	No.	(10)	(95)	(68)	(97)	(20)	(5)	
Bateman's Bay-Montague I.	Range			36-	36-46	45		
	Mean			36.0	39.8	45.0		
	No.			(1)	(12)	(1)		
Tathra Head-Disaster Bay	Range		23-35	27-43	34-47	38-54	49-54	
	Mean		28.1	32.8	39.6	45.6	51.5	
	No.		(102)	(80)	(62)	(11)	(2)	
Samples from trawlers	Range		26-34	28-41	33-51	38-56	43-59	56-59
	Mean		29.9	34.9	40.0	45.9	53.1	57.3
	No.		(49)	(140)	(385)	(139)	(26)	(3)

Figure 12 suggests that the low *K* values subsequent to spawning may be correlated with an increase in translucent growth by the otolith in the subsequent months of April and May. Translucent growth at this time probably accounts for much of the confusion in flathead otoliths.

(iv) *Age-groups and Length Frequencies Compared.*—With reasonable confidence in the age determinations, one of the first steps was to dissect some typical length frequency curves into their constituent age-groups. To this end several large collections of otoliths were made on homogeneous material.

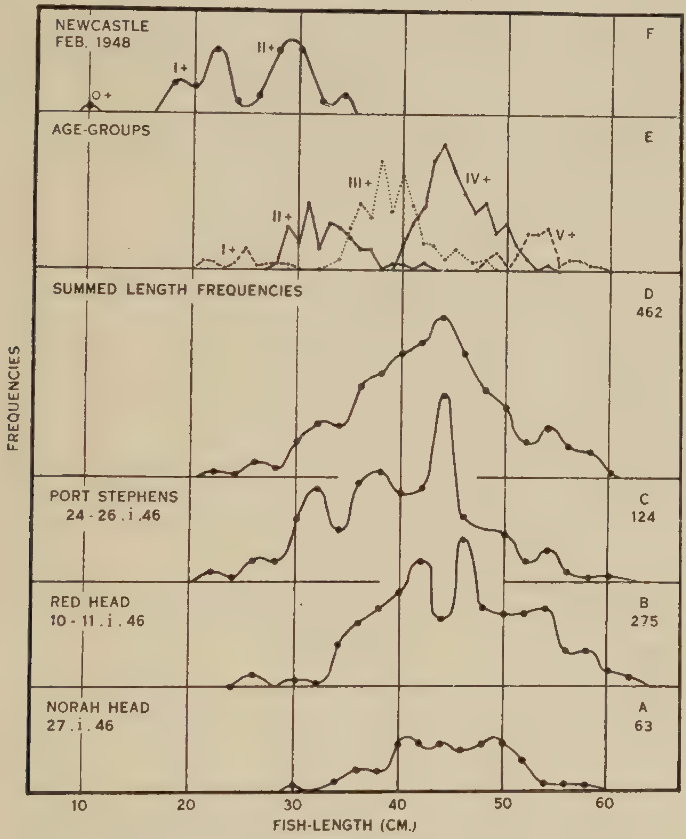

Fig. 18.—Length frequency and age analysis of the flathead catch of a single trawler operating in three neighbouring areas in January 1946. For comparison, the length frequencies of the early age-groups as obtained by experimental trawling in this area in February 1948, using a fine-mesh cover over the codend, are given in *F*.

Figure 18 illustrates an analysis of otolith samples taken from the flathead catch of a steam trawler on two consecutive trips in January 1946, during which three localities were fished, all within 45 miles of one another. The length frequencies from the three localities (*A*, *B*, and *C*) are graphed separately and summed (*D*), using 2 cm. size-groups, the points being joined by curves drawn by eye. Above these graphs are the component age-groups summed (in this case, to avoid any bias, 1 cm. groups were used and the points joined by straight lines). Otoliths were the only material collected on this trip, so the length frequency curves actually are the sum of the age-group polygons. For the sake of clarity, the few VI- and VII-group flathead are not indicated in the age-group diagram. The total number of otoliths in the samples is 462.

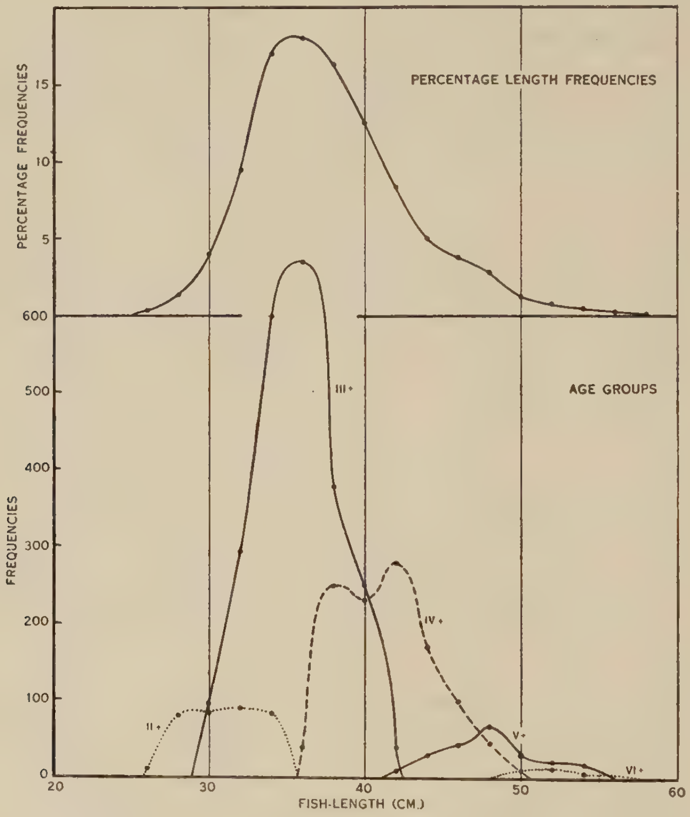

Fig. 19.—The routine market samples of flathead of January 1946 analysed into length frequencies, and age-groups "weighted" by the length frequencies.

The length frequency curves fail to show any clear indication of the age-groups. The curve for the Port Stephens samples (*C*) does show three major modes roughly corresponding with the II-, III-, and IV-groups; but reliance on these could be most misleading. The single large mode in the curve of the summed frequencies (*D*) from 35 to 45 cm. in fact represents two age-groups, though there is no suggestion from the lengths alone of any such division; minor modes above and below this are, however, indicated and represent age-groups.

It is interesting to compare the frequency curves of the very young age-groups obtained experimentally in February 1948 in much the same area (off Newcastle) in Figure 18*F*. Allowances must be made for possible differences in growth between years, but there is clear general agreement between the II-group in each. The I-group of the 1946 material is presumably strongly biased by net selection. Taken together, the two sets of data illustrate the general distribution of the age-groups throughout the size range of flathead, at one time of year.

Some aspects of the age-group polygons are perhaps not very convincing. The extension of the II-group beyond 38 cm., and the similar extension of the III-group up to 48 cm. are certainly open to doubt. But the numbers concerned are low in proportion to the frequencies at those size-groups and would not greatly affect the calculated age composition of the catch. Absolute accuracy is not claimed for the method.

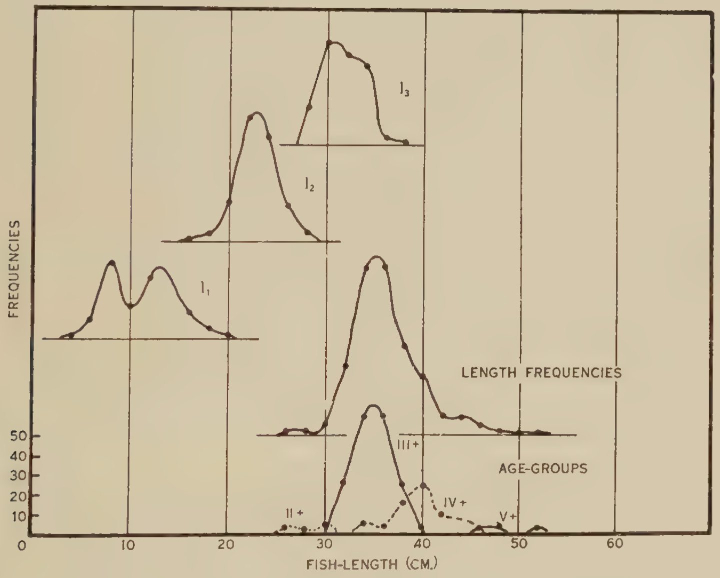

Fig. 20.—A single day's catch of flathead made by one Danish seiner at Brush Island, 30.xi.1945, analysed into length frequencies and age-groups. The calculated intermediate lengths of the III-group are shown in the three upper graphs.

In Figure 19 the full market samples for January 1946 are treated in the manner that will be used for determining the monthly age composition of the total flathead catch. The data comprise 531 age determinations and 3,849 length measurements from samples derived from many parts of the coast. The length frequency curve has been drawn direct from the length data, but the age-group curves have been drawn by determining the proportion of each age-group at each size-group and then "weighting" these in accordance with the length frequencies.

In this way the apparently homogeneous length frequency curve is subdivided into the component age-groups. The bimodal character of the II-group is no doubt due to disproportionate selection of the larger II-group fish by the net. The bimodality of the IV-group is not unexpected from what has gone before. The few VII-group specimens have been omitted from the age-group curves.

Figure 20 represents the entire catch of a single Danish seiner working in one locality on one day. The catch was made at Brush Island on November 30, 1945, and consisted of 325 flathead, all of which were otolithed. Again, the otoliths convincingly subdivide the total length frequency curve. In this case they were read without reference to a length frequency curve, and before it had been constructed.

The bulk of this sample consisted of III-group fish, and the calculated intermediate length frequencies of this age-group are also graphed. The l_1 curve is very ragged and spread out, which, as mentioned above, is to be expected from the protracted spawning of the flathead in any one locality (November-March in this area). The curves of the other intermediate lengths are relatively compact. This may be an effect of growth compensation but is possibly due to the reluctance of the reader to interpret an otolith in such a manner as to obtain very high or very low values for an intermediate length. The data of Figure 15 were not available at the time these particular intermediate lengths were calculated, and Figure 15 is therefore a gratifying check on the earlier work.

TABLE 11

AVERAGE INTERMEDIATE LENGTHS (CM.) IN DIFFERENT AGE-GROUPS OF NEW SOUTH WALES AND TASMANIAN MATERIAL

	Age-group	Intermediate Lengths							Approx. No. in Sample
		l_1	l_2	l_3	l_4	l_5	l_6	l_7	
New South Wales material 1946-47 and 1947-48	II	9.0	23.4						335
	III	8.2	21.8	30.9					470
	IV	8.2	21.3	30.6	37.3				600
	V	8.4	20.8	30.2	37.0	43.9			155
	VI	8.3	20.9	30.9	38.3	44.8	49.7		30
	VII	7.6	21.7	30.3	35.8	42.5	48.3	50.9	3
	Mean:	8.3	21.6	30.6	37.1	43.7	49.0	50.9	
Tasmanian material	II	8.9	22.3						10
	III	9.9	21.8	28.3					120
	IV	9.5	21.2	28.7	34.1				170
	V	9.4	20.8	28.2	33.9	38.4			180
	VI	10.3	20.9	30.0	34.8	43.2	46.0		13
	VII	10.6	20.0	27.4	33.6	39.3	44.2	48.2	2
	Mean:	9.8	21.2	28.5	34.1	40.3	45.1	48.2	

(c) *The Calculated Intermediate Lengths*

The frequency distribution of some typical intermediate lengths has been referred to above. Nothing further may be got from graphing their distributions and in this section average or mean values will be dealt with. These supply the most convenient data from which to examine some dispersive factors in the growth of the flathead, such as those due to locality and sex.

(i) *Lee's Phenomenon.*—Since Lee's phenomenon (of apparent slower growth in the early age-groups of the older fish) is a possible source of error, it must be dealt with first. The average intermediate lengths in the different age-groups of market samples from three localities (Sydney, Ulladulla, and Eden) in the years 1946-47 and 1947-48 are given below (Table 11), with similar values obtained from the Tasmanian samples.

TABLE 12

MEAN INTERMEDIATE LENGTHS (CM.) OF SPECIMENS TAKEN BY EXPERIMENTAL TRAWLING, 1947-48

Locality	Age-group	Intermediate Lengths		
		l_1	l_2	l_3
Newcastle-Port Stephens	I	9.6 (46)		
	II	9.0 (112)	23.3 (118)	
	III	8.6 (40)	24.4 (42)	31.4 (42)
Broken Bay-Port Hacking	I	11.5 (53)		
	II	12.2 (55)	21.5 (23)	
	III	12.2 (6)	22.2 (10)	29.8 (5)
Jervis Bay-Brush I.	I	7.9 (130)		
	II	8.5 (150)	21.5 (151)	
	III	10.0 (37)	22.3 (37)	30.0 (37)
Montague I.-Disaster Bay	I	8.9 (169)		
	II	8.1 (286)	20.5 (317)	
	III	9.1 (40)	20.8 (44)	29.6 (43)

Making allowance for some age-groups represented by inadequate numbers, the phenomenon is well marked in the l_1 and l_2. The differences between l_1 in the various age-groups cannot be due to heterauxetic growth of the otolith. Disproportionate growth below a fish-length of 10 cm. would cause the average calculated value of l_1 to be higher than the actual average fish-length it represents, but this discrepancy should be the same in all subsequent age-groups. The most likely cause of Lee's phenomenon in this case is the differential catching of the young, fast-grown specimens, while the slow-growing individuals are spared for a time. This could operate either by the smaller individuals not moving out into the deep water as soon as the larger specimens of the same age (and sex), or by the smaller individuals escaping through the meshes of the codend.

During the experimental trawling with a fine-meshed cover over the codend there was no escape by specimens larger than 10 cm. In Table 12 are given the mean intermediate lengths of all specimens obtained during this work, up to the III-group, divided into four localities. The samples were obtained between June 1947 and December 1948. Figures in brackets represent the numbers in the sample.

There is here no consistency in the variations of l_1, and therefore no evidence of Lee's phenomenon. With l_2 there is consistent variation, but of the opposite nature to that of Lee's phenomenon. Whatever the cause of this variation in l_2, it is evident that the occurrence of Lee's phenomenon in the flathead is fully explained by the differential catching of the fast-grown individuals, and that the disproportionate growth of the otolith is fully compensated for by the correction applied (Section III (*a*) (iii)).

TABLE 13

AVERAGES OF MEAN INTERMEDIATE LENGTHS (CM.) OF ALL AGE-GROUPS
(Figures in brackets represent the numbers in the samples)

Locality	Mean Intermediate Lengths						
	l_1	l_2	l_3	l_4	l_5	l_6	l_7
1946-47							
Broken Bay-Port Hacking	9.4 (319)	22.4 (325)	31.8 (336)	38.1 (224)	45.6 (62)	50.0 (17)	50.9 (1)
Jervis Bay-Brush I.	9.0 (190)	21.5 (230)	30.6 (214)	37.3 (119)	45.1 (19)	50.1 (9)	
Tathra Head-Disaster Bay	8.9 (402)	21.9 (428)	30.2 (385)	36.8 (223)	43.0 (53)	44.9 (1)	
1947-48							
Broken Bay-Port Hacking	7.7 (211)	23.4 (236)	30.2 (42)	37.1 (30)	43.5 (11)	47.8 (2)	50.9 (1)
Jervis Bay-Brush I.	8.5 (234)	21.8 (258)	31.1 (180)	37.9 (117)	42.3 (22)	49.7 (4)	
Tathra Head-Disaster Bay	7.8 (168)	21.1 (157)	29.9 (117)	36.4 (60)	41.8 (12)	46.9 (1)	
Marion Bay (Tasmania)	9.8 (482)	21.2 (621)	28.5 (610)	34.1 (467)	40.1 (191)	45.1 (15)	48.2 (1)

(ii) *Growth Differences Due to Locality.*—It is already clear from Table 12 that there is a locality difference in the growth rate of the flathead. The fish from the northern localities grow fastest and those in the south slowest. These differences can also be examined in the market samples. In most of the samples obtained from Danish seiners the locality of origin is known. The averages of the mean intermediate lengths of all age-groups of the flathead from three localities in two years are given below in Table 13, together with means of the samples from Tasmania obtained in 1944 and 1945. By taking the average of the means of all age-groups, some of the discrepancies due to Lee's phenomenon should cancel out.

The fuller 1946-47 material has been plotted in Figure 21 together with the Tasmanian material. The curves have not been produced to the origin, since the first increment does not represent a full year's growth.

The differences in growth rate shown by this figure are not great, but they are consistent over a number of years. Values from the Newcastle-Port Stephens area are excluded because few specimens occur in the market material, but from the foregoing section it is evident that fish from this area grew faster. The growth rate difference exhibited by the Sydney and Ulladulla samples in their early intermediate lengths is apparently not maintained; this possibly indicates a gradual mixing of the stock of older flathead of the two areas (see section on populations of the flathead). The later mean intermediate lengths of the Tasmanian samples are also perhaps being increased through dilution of the local stock by fish from Bass Strait. The Marion Bay samples in any case represent the extreme southern limit of the flathead range and are included only to stress the pattern of decrease in growth rate from north to south.

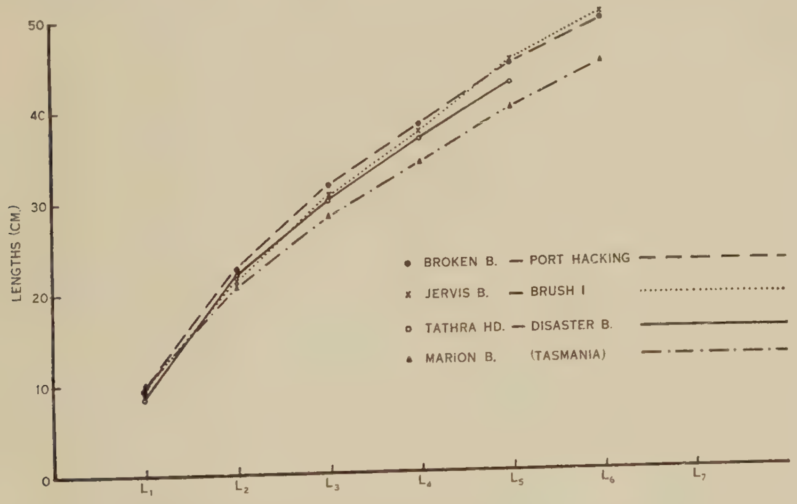

Fig. 21.—The growth rate of the flathead by localities, from the mean calculated intermediate lengths of the 1946-47 market material. The material from Tasmania is also included. Data in text.

An independent check is provided by a comparison of the actual mean fish-lengths from the localities. These means are subject to great sampling errors, and the II- and III-groups are badly affected by net selection. However, in Tables 9 and 10 are given the mean fish-lengths of each age-group from each locality in 1946-47 and 1947-48. The results are not clear-cut, but in the IV- and V-groups and where the sample sizes appear adequate, there is a fairly consistent trend agreeing with the calculated intermediate lengths.

(iii) *Growth Differences Due to Sex.*—The growth rates of the sexes were compared by analysing the 1946-47 market samples of known sex. As in the preceding section, these samples were in all cases read in ignorance of the sex of the individuals. The results are set out in Table 14, in which the material is dissected for locality, and the mean fish-lengths of each age-group are given with the mean calculated intermediate lengths. The mean fish-lengths are a more direct means of comparison but are subject to large sampling errors. The mean calculated intermediate lengths have therefore been used in Figure 22, taking the average of the mean values of the localities, only omitting the values for the Newcastle samples, of which there were very few.

TABLE 14

GROWTH RATE OF THE SEXES: 1946-47 MARKET SAMPLES
(Figures in brackets represent the numbers in the sample)

Localities	Mean Fish-length of Each Age-group								
	Males				Females				
	II	III	IV	V	II	III	IV	V	VI
Port Stephens-Newcastle	—	34.8 (2)	—	—	—	35.8 (1)	36.8 (1)	—	—
Broken Bay-Port Hacking	30.1 (2)	36.9 (19)	42.0 (23)	45.7 (4)	32.3 (2)	38.1 (26)	43.2 (44)	49.7 (8)	44.7 (7)
Jervis Bay-Brush I.	32.2 (4)	33.9 (15)	39.1 (13)	43.2 (3)	33.3 (1)	36.3 (14)	41.3 (22)	44.7 (5)	52.1 (3)
Bateman's Bay-Montague I.	—	36.7 (5)	44.5 (6)	43.1 (7)	—	38.7 (5)	45.0 (5)	45.5 (5)	49.6 (1)
Tathra Head-Disaster Bay	29.9 (5)	33.1 (21)	37.1 (10)	44.2 (1)	30.0 (4)	35.5 (4)	40.2 (18)	46.4 (9)	—

	Mean Intermediate Lengths										
	Males					Females					
	l_1	l_2	l_3	l_4	l_5	l_1	l_2	l_3	l_4	l_5	l_6
Port Stephens-Newcastle	11.0 (1)	25.0 (2)	33.2 (2)			9.9 (2)	22.3 (2)	31.7 (2)			
Broken Bay-Port Hacking	11.1 (50)	22.2 (49)	31.1 (48)	37.3 (27)	42.3 (3)	11.3 (76)	23.4 (83)	32.3 (82)	39.4 (56)	46.6 (15)	51.3 (6)
Jervis Bay-Brush I.	10.8 (26)	22.3 (31)	30.5 (28)	36.1 (10)	41.9 (4)	10.8 (41)	22.9 (43)	31.5 (39)	37.8 (28)	43.7 (7)	50.8 (3)
Bateman's Bay-Montague I.	11.2 (16)	22.7 (16)	31.1 (17)	37.7 (11)	41.7 (6)	10.0 (14)	21.9 (12)	31.6 (16)	38.0 (10)	41.6 (5)	48.2 (1)
Tathra Head-Disaster Bay	11.6 (33)	21.7 (36)	29.5 (30)	35.1 (11)	43.2 (1)	11.2 (46)	23.1 (43)	31.1 (40)	37.3 (29)	43.9 (8)	—
Average of means	11.2	22.2	30.6	36.6	42.3	10.8	22.8	31.6	38.1	44.0	50.1

It is evident that there is a small but consistent difference in the growth rates. The males, as usual, are the slower grown, and at a calculated length of 40-45 cm. the females are 1.5-2 cm. larger. The differences in the actual lengths shown in Table 14 are somewhat larger, particularly in the III-group, where the females are 2 to 2.5 cm. larger. The difference between the sexes in the l_1, where the males appear to be the larger, was tested for the III-group alone (the most numerous) and the result shown in Table 15 was obtained.

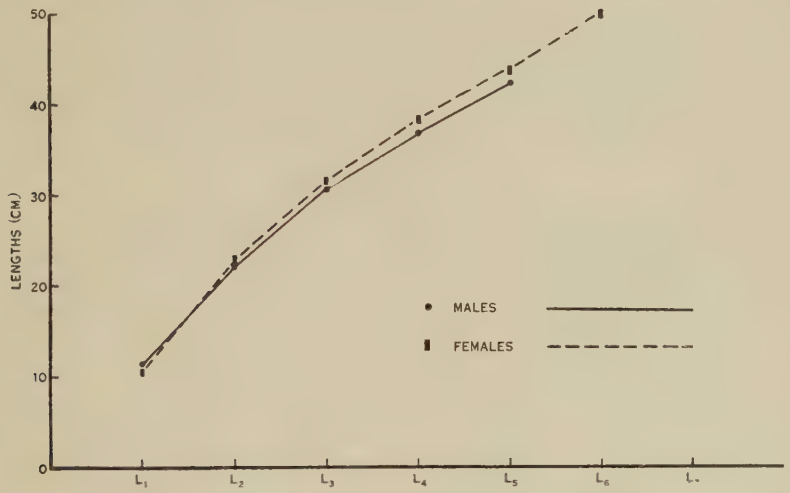

Fig. 22.—The growth rate of the sexes of the flathead; average values derived from the mean calculated intermediate lengths of the localities in the 1946-47 market material. Data in Table 14.

The difference between the averages is highly significant, the females having the higher l_1. The contrary result indicated by the averages in Table 14 no doubt results from the greater depressive effect of Lee's phenomenon on the early calculated intermediate lengths of the female fish, owing to the much greater numbers of old females than old males.

TABLE 15

MEAN l_1 IN MALES AND FEMALES FROM THREE DIFFERENT AREAS

	Mean l_1	
	Males (cm.)	Females (cm.)
Broken Bay-Port Hacking	10.3	11.4
Jervis Bay-Brush I.	11.3	11.6
Tathra Head-Disaster Bay	9.5	11.5
Average	10.3	11.5

(iv) *Growth Rate from the Scales.*—At the commencement of this investigation scales were studied. Calculated intermediate lengths from the scales must be regarded as unreliable until the proportional growth of scale and fish has been determined. From a fish-length of 25-55 cm., growth is isauxetic in the flathead, but below 25 cm. there are no data and the slope of the line indicates considerably faster growth of the scale in the first year or two. The intermediate lengths calculated from the scales are, in fact, in substantial agreement with those calculated from the otoliths. There is a tendency in scales to form supernumerary annuli within l_1 as in the otolith. Subsequent true annual annuli are difficult to identify because of supernumerary annuli. Scales were therefore rejected for this study but they might prove useful if used in conjunction with otoliths if ever a suitable tagging method for flathead can be devised.

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EXPLANATION OF PLATES 1-4

PLATE 1

Samples of flathead ovaries broken up and photographed without staining. Figures 1 and 2 magnified about 50x; Figures 3-6 magnified about 14x.

Fig. 1.—Early stage III ovary, barely pigmented, 2 g., 2.vii.48. Mostly group (*a*) ova; a few group (*b*) ova, very few of which are as large as 0.2 mm. diameter.

Fig. 2.—Late stage III ovary, 7 g., 25.vi.48. Numerous group (*b*) (pigmented) ova varying up to 0.2 mm. diameter.

Fig. 3.—Early stage IV ovary, 14 g., 21.x.48. Mostly group (*c*) ova of various sizes. Groups (*a*) and (*b*) also present.

Fig. 4.—Typical stage IV ovary, 43 g., 30.viii.48. Full-grown group (*c*) ova, as well as small group (*c*) and numbers of groups (*a*) and (*b*).

Fig. 5.—Late stage IV ovary, 109 g., 2.xi.48. Group (*c*) ova of the largest size, as well as smaller ones.

Fig. 6.—Full, stage VI ovary, 77 g., 26.i.49. Large group (*c*) ova have suddenly increased in size to group (*d*), and are translucent with the oil globule clearly visible. Group (*c*) ova of all sizes are still present in large numbers.

a., group (*a*) ova; a_1., group (*a*) ova that have not been broken up and are still held together by ovarian tissue; *b*., group (*b*) ova; *c*., group (*c*) ova; c_1., small group (*c*) ova (it is uncertain whether these ova would develop and be spawned in the current season); *d*., group (*d*) ova (mature, ready for spawning); o.g., oil globule.

PLATE 2

Flathead Otoliths

Fig. 1.—Fish-length 31 cm., collected off Port Hacking, 2.vii.47. Three translucent zones, the last one having been just formed.

Fig. 2.—Fish-length 35 cm., collected off Red Head, 13.viii.47. Three translucent zones, as in No. 1, but with a very narrow band of opaque growth beyond the last.

Fig. 3.—Fish-length 38 cm., collected off Cape Hawke, 23.x.48. Three translucent zones with a fourth, probably supernumerary, annulus at the edge.

Fig. 4.—Fish-length 34 cm., collected off Newcastle, 11.ii.48. For interpretation, see Section III (*a*) (ii).

Fig. 5.—Fish-length 51 cm., collected off Port Stephens, 25.i.46. Five translucent annuli, the fourth opaque zone being split by a supernumerary annulus. *a* and *b* mark the two measured axes of the otolith, and the anterior, posterior, ventral, and dorsal margins are marked.

Fig. 6.—The right otolith as it would be seen from above, lying in the otic cavity.

Plate 3

Flathead Otoliths

1, 2, and 3 collected off Red Head, 21.x.48.
4, 5, and 6 collected off Eden, 12.x.48.

1.	I+ fish	17 cm.	17 cm.
		18 cm.	20 cm.
2.	II+ fish	25 cm.	25 cm.
		26 cm.	26 cm.
3.	III+ fish	34 cm.	34 cm.
		35 cm.	
4.	I+ fish	13 cm.	13 cm.
		13 cm.	13 cm.
5.	II+ fish	21 cm.	21 cm.
		20 cm.	22 cm.
6.	III+ fish	34 cm.	34 cm.
		36 cm.	36 cm.

Plate 4

Flathead Otoliths

Fig. 1.—Fish-length 42 cm., collected 11.xii.41. IV+, with a fifth annulus forming on the edge. A supernumerary annulus (*s*) in the second opaque zone.

Fig. 2.—Fish-length 31 cm., collected 5.ii.42. III+, with a fourth annulus forming on the edge, and a supernumerary annulus (*s*) in the third opaque zone. The anterior tip of this specimen is broken off.

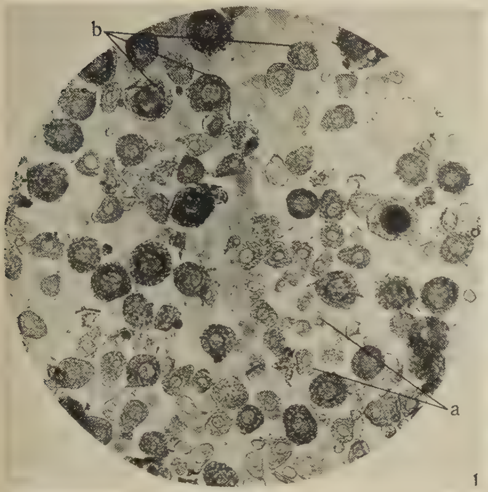
Fig. 3.—Fish-length 34 cm., collected 5.ii.42. III+, with second annulus omitted.

Fig. 4.—Fish-length 46 cm., collected Jervis Bay 10.ix.48. V+, clearly marked, the fifth annulus being just inside the edge, which shows a little opaque growth; "larval annulus" marked *l.a.*; a tendency to form supernumerary annuli in the third and fourth opaque zones.

Fig. 5.—Fish-length 30 cm., collected off Lakes Entrance (Vic.) 23.viii.48. II+, with "larval annulus".

Fig. 6.—Fish-length 35 cm., collected 28.ix.48. III+, with new growth just begun, and "larval annulus".

NEW SOUTH WALES TIGER FLATHEAD. I



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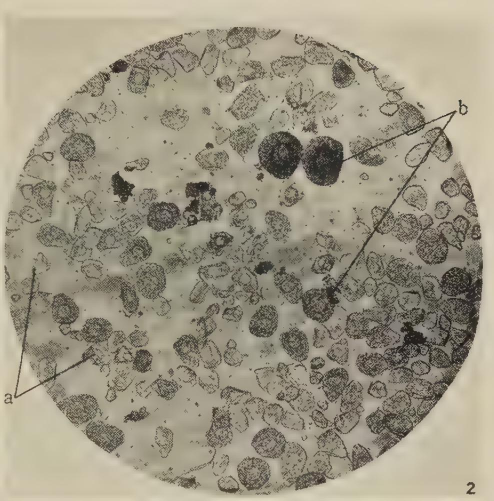

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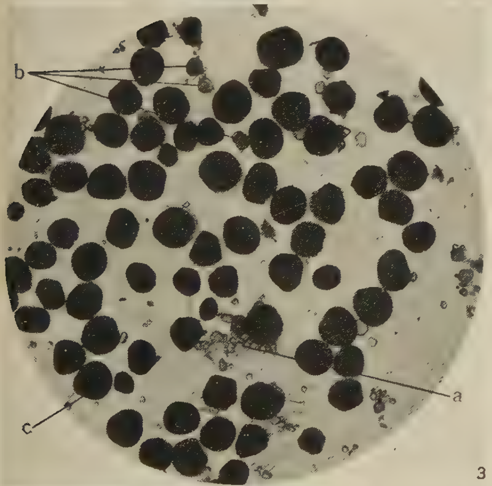

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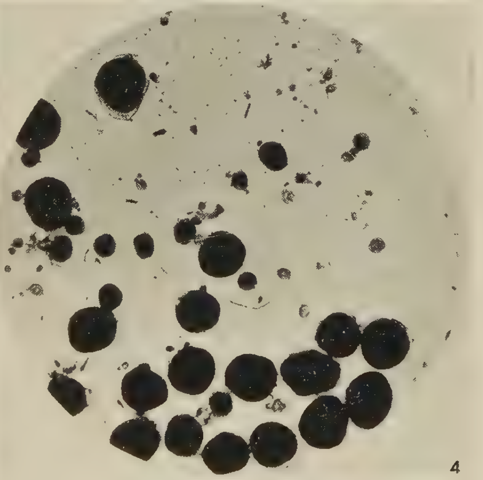

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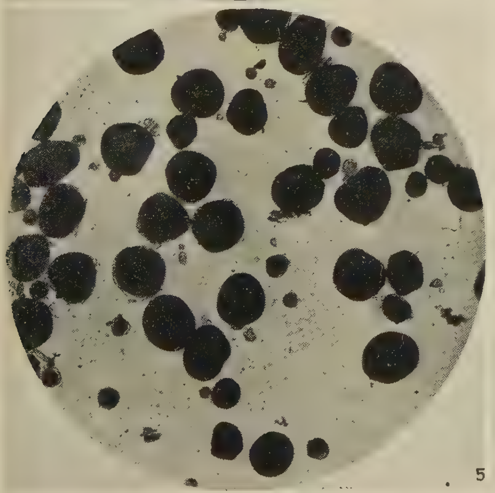

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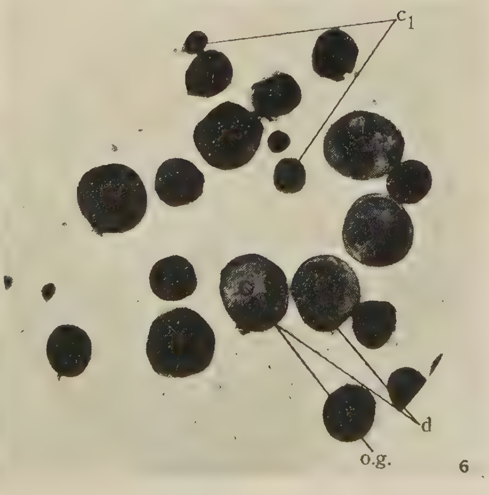

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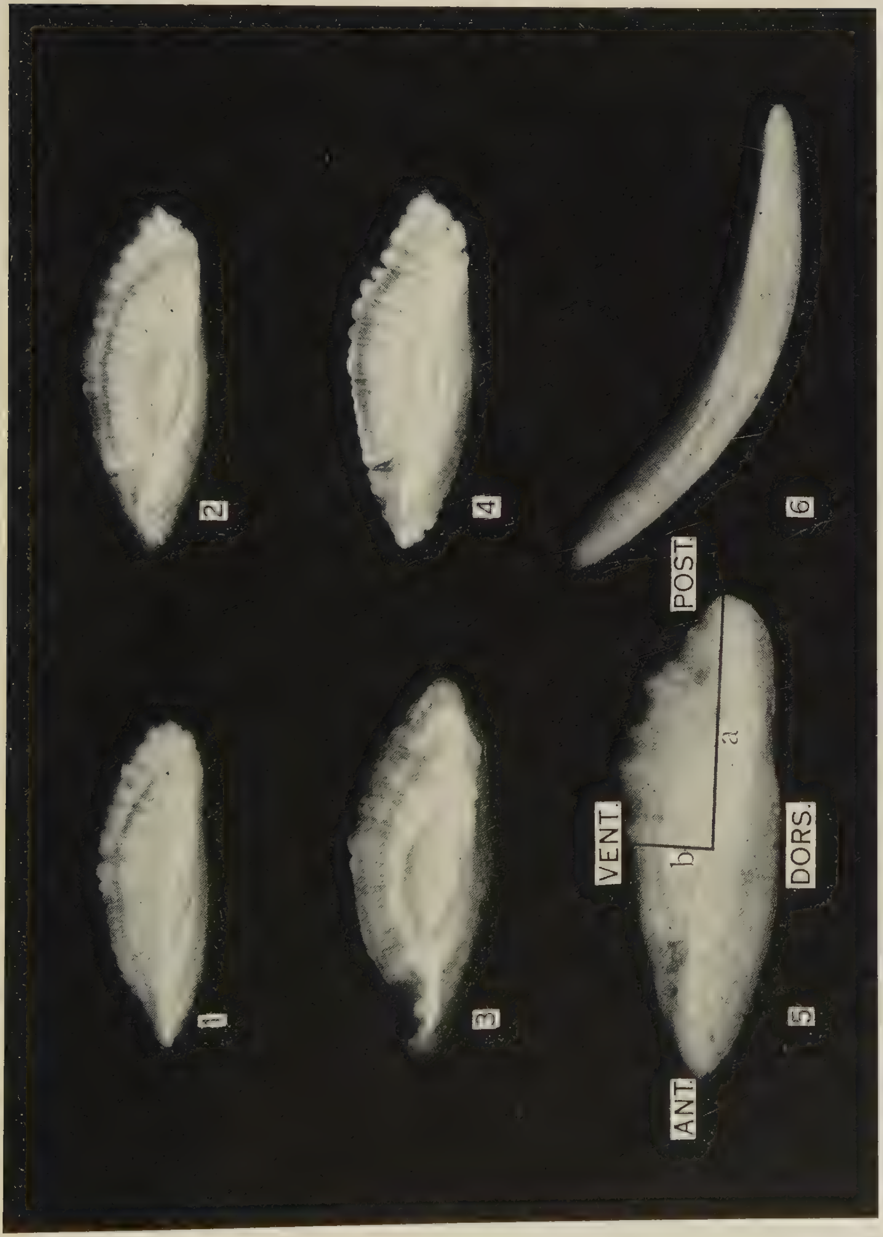
PLATE 2



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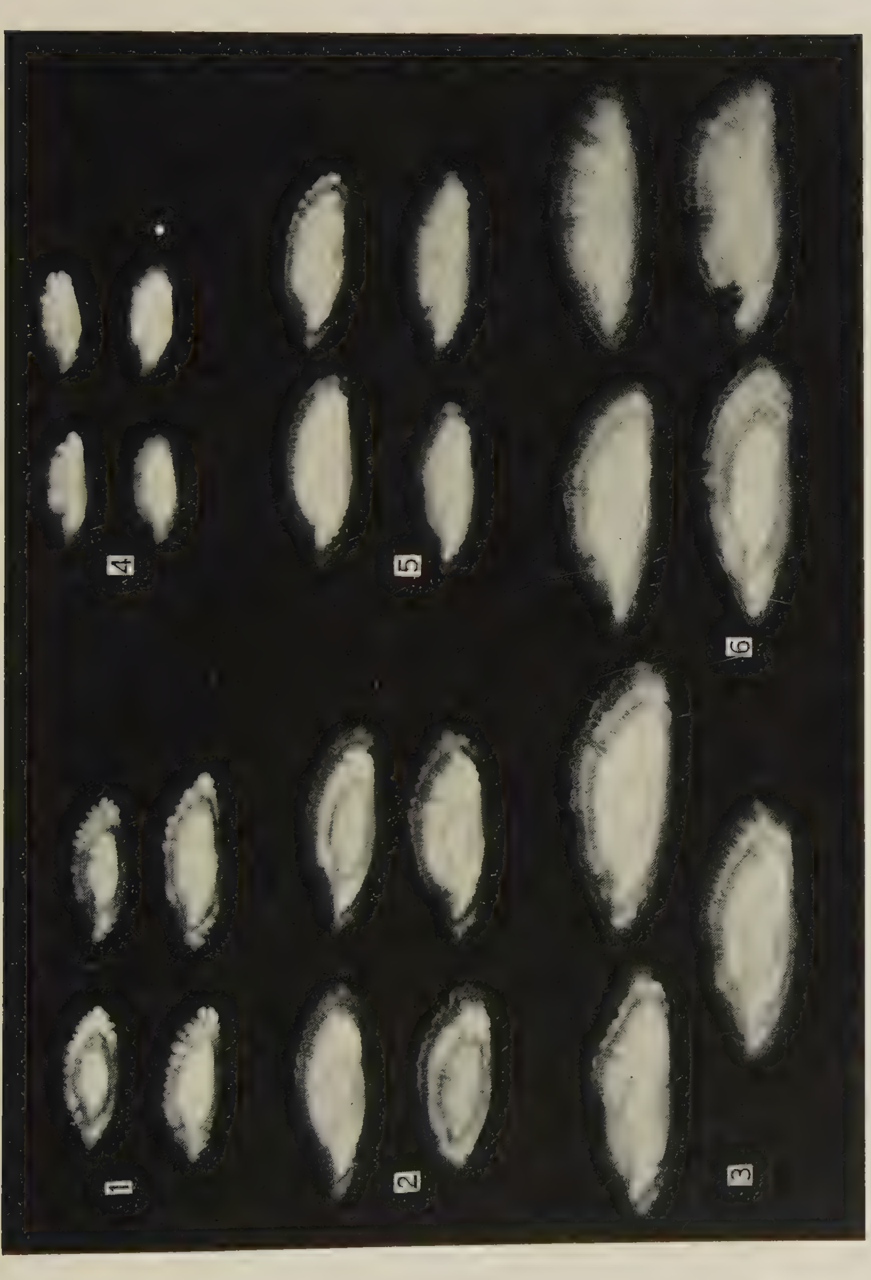

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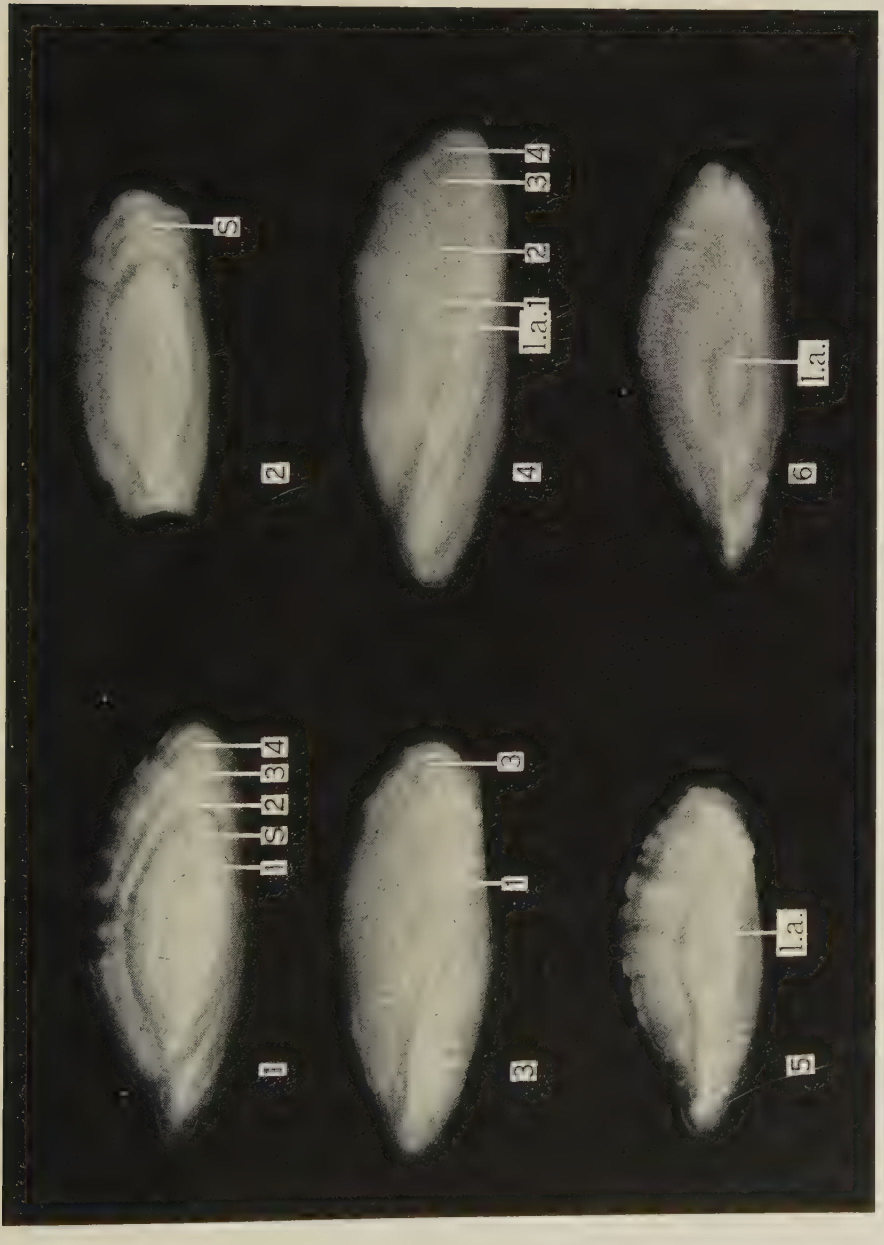

RACES AND POPULATIONS OF THE AUSTRALIAN PILCHARD, *SARDINOPS NEOPILCHARDUS* (STEINDACHNER)

By M. Blackburn*

(*Manuscript received March* 31, 1951)

Summary

The evidence of taxonomic differentiation in the Australian pilchard is reviewed. Three major groups (called races), located respectively in eastern, south-eastern, and south-western Australian waters, are distinguished by differences in growth rate. The boundary zone of the two former is near the New South Wales-Victoria border, but it is not certain to which of the two latter races the South Australian fish belong. The two former races are subdivided into smaller, more or less separate stocks (populations), which are distinguished mainly by differences in mean number of vertebrae and in abundance fluctuations. There are at least two such groups in the eastern race, which meet between Port Jackson and Jervis Bay, and at least two in the south-eastern race. The pilchards of Cook Strait, New Zealand, are probably distinct from those of any Australian locality.

I. Introduction

The pilchard, *Sardinops neopilchardus* (Steindachner), occurs in the coastal waters of Australia south of the Tropic of Capricorn, including Tasmania and New Zealand. An attempt was made to study the biology of the species throughout its Australian range, with the results reported in previous papers (Blackburn 1941, 1949, 1950*c*; Blackburn and Tubb 1950). Because of the immensity of the range and the lack of any organized fishery, more observations were made in some areas than in others. The assembled facts have shown that there is more than one stock of the species in Australian waters. However, the point was not particularly emphasized in the earlier papers, although it was borne in mind when presenting the information in them, nor was all the available evidence then discussed. In this paper all the facts indicative of heterogeneity in the species are reviewed, and conclusions are drawn as to the distribution of the recognizable intraspecific groupings.

II. Evidence of Heterogeneity

(*a*) *Restriction of Random Interbreeding*

This was discussed by Mayr (1942, Chap. 9) in his classification of isolating mechanisms. If some individuals have little or no opportunity to interbreed with others of the same species, the respective groups are more or less isolated biologically, even though they may be in contact geographically. Such restricted interbreeding opportunity can occur when there are differences in the seasons of reproduction.

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On the eastern coast of Australia, north of the Victoria-New South Wales border (Fig. 1), the pilchard spawning season lasts from about mid autumn to mid spring. However, the main season at any locality is shorter, and is progressively later in more northern localities: late autumn in southern to central New South Wales, winter in central to northern New South Wales, and early spring in northern New South Wales and southern Queensland (Blackburn 1941).

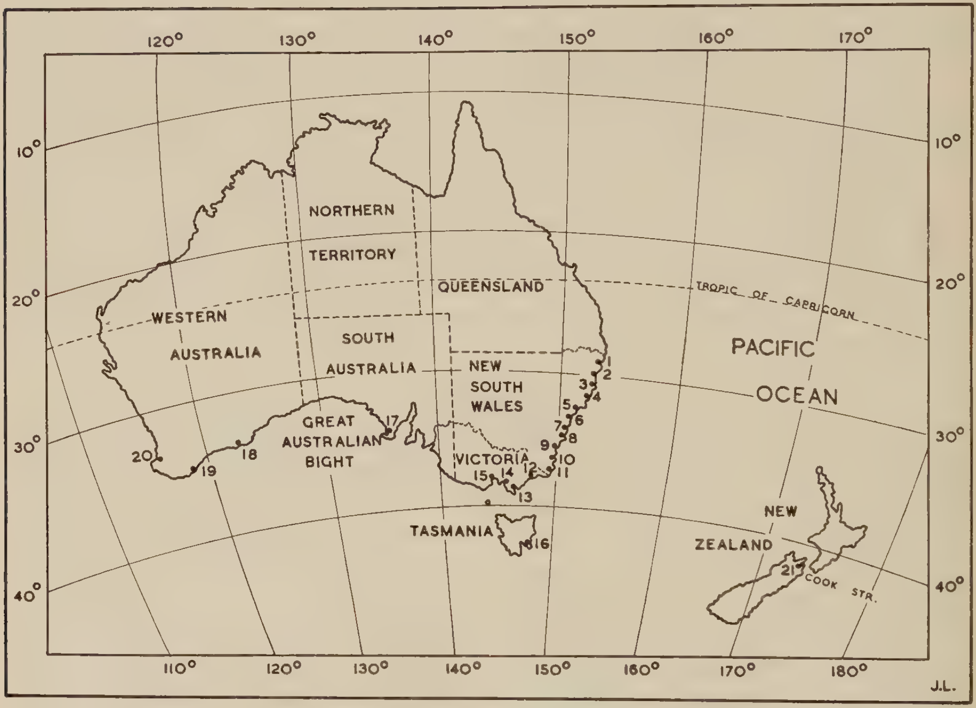

Fig. 1.—Australia and New Zealand, showing locality numbers identified in Table 1.

In the south-eastern waters, on the other hand, the reproductive season is in the warmer part of the year, though again varying with locality. At Lakes Entrance in eastern Victoria, near the New South Wales border, the main spawning season is the spring and early summer; further west at Port Phillip Bay it is the late spring and summer; while in South Australia, still further west, it occurs in summer and autumn. The data for Tasmania are meagre, but they indicate some spawning in summer, possibly extending into autumn (Blackburn 1950*c*).

On the south coast of Western Australia the main spawning season is in the autumn and winter (Blackburn 1950*c*). The season on the western coast is not definitely known.

It would not be impossible to associate the minor gradational differences in spawning time, for example between adjacent localities on the eastern or south-eastern coasts, with a hypothesis of homogeneity of stock in the localities concerned. But the broad spawning seasons that characterize the three main areas mentioned above— winter in eastern Australia, summer in the south-east, and winter in the south-west—are so different as to make completely random interbreeding over the entire Australian range seem quite impossible. Further, although there is an extensive overlapping in autumn of the spawning seasons in the south-eastern and south-western areas, which could permit some exchange of spawners between them, there is no such overlapping between the seasons in the south-eastern and eastern areas. In eastern Victoria spawning is at its height in spring, while in the adjacent area of southern New South Wales this stage is reached in autumn.

It could still be argued that this restriction of interbreeding opportunity might not be operative over the whole adult life of the fish. For example an individual might during its lifetime spawn once or more often in each of the three main areas at the appropriate seasons, although the supposition is rather at variance with the general closed-circle theory of fish life history and migrations (Russell 1937). In this event the fish would not spawn at regular annual intervals. An extensive study of pilchard scales, particularly of those from New South Wales and Victorian waters, has shown that certain rings register spawnings and that these rings are all formed at much the same season in material of a given area (Blackburn 1949, 1950*c*). It is thus almost certain that adult pilchards spawn annually, at the season appropriate to the area in which they live, and that large-scale exchanges of spawners do not take place over the range of the species.

Groups that are partly or wholly isolated as breeders may be expected to differ in morphological or physiological characters (Dobzhansky 1937, Chaps. 5, 6; Huxley 1942, Chap. 5). Such differences are more reliable and useful, as indicators of heterogeneity, than are observations on probable isolating mechanisms. They are discussed below for this species. The recognition of isolating mechanisms is nevertheless of great importance in fish biology. The identification of different groups is a gradual process that frequently cannot be completed until other biological work on the species is well advanced. This applies particularly to age determination studies, which may yield distinguishing characters directly (growth rate differences) or which may be important in analysis of morphological characters (e.g. effects associated with year-class in vertebra number variation). But studies such as age determination, in a widely ranging species, must involve some grouping of data from different localities if excessively detailed work is to be avoided. Indications of isolating mechanisms may provide a basis for judicious grouping of this kind at an early stage in an investigation. This was done with great advantage in the Australian pilchard work. It is also being done in the work on barracouta (*Thyrsites atun*).

The European *Sardina pilchardus* spawns in winter and summer in the warmer and colder parts of its range respectively (Blackburn 1949

TABLE 1

RAW DATA AND STATISTICS OF PILCHARD VERTEBRAL COUNTS, ALL SAMPLES FROM EACH LOCALITY COMBINED

Locality	Vertebrae									*N*	*A.M.*	*S.D.*	*S.E.*	Samples of 50 or More Fish		
	45	46	47	48	49	50	51	52	53					No.	Range of Means	Range of Seasons of Collection
1 Byron Bay (N.S.W.)				11	27	49	13			100	49.64	0.847	0.085	1	49.64	1948
2 Nambucca R. (N.S.W.)					16	69	14	1		100	50.00	0.586	0.059	1	50.00	1940
3 Camden Haven (N.S.W.)			2	5	23	72	11			113	49.75	0.762	0.071	1	49.68	1940
4 Port Stephens (N.S.W.)	1			4	21	70	15			111	49.83	0.819	0.078	1	49.82	1939
5 Bird I. (N.S.W.)		1		10	27	53	12	2		105	49.67	0.937	0.090	1	49.67	1939
6 Port Jackson (N.S.W.)				8	91	285	58	1		443	49.89	0.638	0.030	3	49.73-50.07	1948-1949
7 Kiama (N.S.W.)					19	69	14	1		102	49.95	0.569	0.056	1	49.95	1949
8 Jervis Bay (N.S.W.)				2	30	192	44	1		269	50.04	0.565	0.034	1	49.97	1940
9 Bateman's Bay (N.S.W.)				1	19	70	24	7		121	50.14	0.778	0.071	1	50.07	1940
10 Wagonga R. (N.S.W.)				1	23	68	10			102	49.85	0.587	0.058	1	49.85	1939
11 Twofold B. (N.S.W.)				6	48	244	61	12	1	372	50.08	0.712	0.037	4	49.92-50.45	1940-1945
12 Lakes Entrance (Vic.)				4	84	262	63	3		416	49.94	0.647	0.032	4	49.83-50.02	1944-45 to 1945-46
13 Corner Inlet (Vic.)					14	94	18	2		128	50.06	0.558	0.049	1	50.06	1943-44
14 Westernport (Vic.)				1	28	146	34			209	50.02	0.563	0.039	2	50.02-50.04	1945-46
15 Port Phillip B. (Vic.)			1	17	332	1093	110	1		1554	49.83	0.556	0.014	13	49.77-50.11	1942-43 to 1948-49
16 Fortescue B. (Tas.)					14	79	19	1		113	50.06	0.571	0.054	1	50.04	1941
17 Coffin Bay (S.A.)				10	97	274	16			397	49.72	0.568	0.029	3	49.55-49.84	1940-1949
18 Lucky Bay (W.A.)					9	81	10			100	50.01	0.438	0.044	1	50.01	1947
19 King George Sd. (W.A.)				5	46	186	14			251	49.83	0.540	0.034	1	49.82	1948
20 Geographe B. (W.A.)					24	77	3			104	49.80	0.470	0.046	1	49.84	1949
21 Queen Charlotte Sd. (N.Z.)					15	130	97	7		249	50.39	0.644	0.041	2	50.33-50.47	1939-1941

and references), thus resembling *Sardinops neopilchardus* in Australia. The spawning season for the latter species in Cook Strait and possibly other New Zealand waters is in spring and summer (Arthur 1883; Phillipps 1921, 1929), which is similar to that in Australian waters at about the same latitude.

(*b*) *Morphological Characters*

(i) *Vertebra Number.*—This character has been widely and successfully used in distinguishing stocks in clupeoid species. The records here refer to total number of vertebrae including the urostyle, and all counts were made by the writer. Abnormal vertebrae, which were very rare, were dealt with by counting the centra only.

Table 1 shows the frequency of occurrence of skeletons with different vertebral counts, for each locality from which 100 or more specimens were available. The number of observations (*N*), mean vertebra number (*A.M.*), standard deviation (*S.D.*), and standard error of mean (*S.E.*) are given. The number of samples of 50 or more fish, the range of means in such samples, and the range of seasons (biological years) of collection are also stated for each locality. The total number of counts is 5,459, including 249 from Queen Charlotte Sound, Cook Strait, New Zealand.

There is an irregular trend in the means of all counts for successive localities. The New Zealand mean, 50.39, is by far the highest. Of the eastern and south-eastern Australian means, those over 49.90 are with one exception confined to localities south of Port Jackson and east of Port Phillip, while, with one exception, the lower means occur only in localities further north and west. The individual sample means show a similar trend, but they indicate considerable variation between samples at the same locality, which explains much of the irregular variation between localities. Some of the variation at the same locality, but not all, is non-significant; the possible causes of significant variation are discussed below.

The means for Port Jackson, Twofold Bay, Lakes Entrance, Port Phillip, and Coffin Bay (localities 6, 11, 12, 15, and 17 in Table 1 and Fig. 1) are all based on more than 300 specimens, including at least three samples of 50 or more collected in at least two seasons, i.e. on a larger and more representative material than are the other means. The New Zealand figure (locality 21 in Table 1 and Fig. 1), which is of special interest, comes next in reliability. The significance of differences between these means can be appraised by the graphical method of Hubbs and Perlmutter (1942), which the present author employed in studying vertebral count variation in the Australian anchovy, *Engraulis australis* (Blackburn 1950*a*). The range, mean, and twice standard error above and below the mean, are shown for each of the six localities (Fig. 2). The rectangles representing standard errors are compared as to relative length and relative separation or overlap, the process yielding *t* values. The New

Zealand mean is significantly different from all the others, of which each is significantly different from those of localities next adjacent. An overall test of the mean vertebral counts for these six localities shows that differences between them are highly significant, thus ensuring that individual comparisons may be validly made. Thus there are probably more or less separate stocks of pilchards in the different areas in which these places are situated.

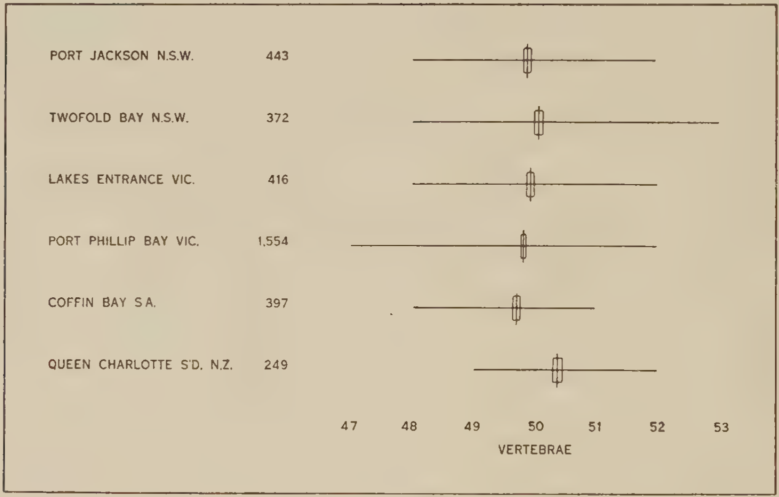

Fig. 2.—Summary of data on vertebral counts of pilchards from certain localities. The numbers of specimens studied from the different localities are shown on the left. For each locality-sample the horizontal line indicates the range, the vertical cross-bar the mean, and the hollow rectangle twice the standard error on each side of the mean. For further explanation see text.

In other clupeoids, including the European and Pacific North American pilchards (*Sardina pilchardus* and *Sardinops caerulea*), certain year-classes may have relatively high or low mean vertebra numbers at the same locality, or even over a series of localities (Tester 1937; Runnström 1941; Navarro 1946; Clark 1947). This indicates that variation in vertebra number is partly non-genetic, a conclusion supported by the results of experiments with other fishes (Gabriel 1944; Tåning 1944). Other possible sources of variation in vertebra number are differences by age in the year-class (Tester 1937), relative size in the age-group (Tester 1937; Molander 1940), and sex (mainly in salmonoids, e.g. Blackburn 1950*b*).

It would therefore be desirable to analyse the variation in vertebra number to separate the locality effects from the other effects which might be responsible for variation. That cannot be done adequately for this material. As shown in previous papers, the material for the Australian pilchard studies only came to hand intermittently over a number of years.

This was because of the virtual absence of fisheries, the limited facilities for procurement from other sources, and fluctuation in abundance and availability.

TABLE 2

MEAN STANDARD LENGTHS (MM.) OF PILCHARDS WITH DIFFERENT VERTEBRA NUMBERS IN HOMOGENEOUS MATERIAL; Sx^2 IS SUM OF SQUARES OF DEVIATIONS FROM MEAN

Sample	49 Vertebrae			50 Vertebrae			51 Vertebrae		
	N	*A.M.*	Sx^2	*N*	*A.M.*	Sx^2	*N*	*A.M.*	Sx^2
Nambucca River 19.i.40. O-group	16	35.88	109.750	69	34.58	536.812	14	35.71	38.857
Jervis Bay 25.x.40. I-group	17	80.00	144.000	63	80.14	1223.713	18	82.17	308.500

There were also difficulties in determining the age of many of the specimens received (Blackburn 1950*c*). Victorian specimens were allocated to age-groups according to scale readings, and New South Wales fish mainly according to size. In the latter area fish in certain size ranges are virtually confined to particular age-groups (Blackburn 1949, see also Blackburn 1950*c*, Section II (*d*) (iii)), and some in adjacent size ranges were also allotted to age-groups where this seemed justified by length frequency distributions (cf. Hubbs 1925; Hart 1937; Clark 1947, who used similar methods for the same kind of analysis). As the size ranges were mostly modal for the age-groups in question, and were identical for the material in any of the pairs compared for vertebra count in Tables 3 to 5, the comparisons cannot be invalidated by any possible correlation between vertebra number and relative size of fish. In any case there is no evidence of this in Table 2, which shows the mean standard lengths of fish with different numbers of vertebrae in two samples in which the length frequency distribution was nearly normal. It can be shown that none of the differences is significant.

TABLE 3

MEAN VERTEBRA NUMBERS COMPARED FOR SEXES IN HOMOGENEOUS MATERIAL

Material	Male			Female			*t*
	N	*A.M.*	Sx^2	*N*	*A.M.*	Sx^2	
Port Stephens, 1937 class, II-group	43	49.74	38.187	47	49.89	22.469	0.86
Wagonga River, 1938 class, I-group	58	49.95	22.845	40	49.75	9.500	1.69
Port Phillip, 1939-40 class, IV-group	120	49.86	32.592	149	49.81	43.359	0.76
Port Phillip, 1940-41 class, III-group	71	49.87	15.860	62	49.71	16.774	1.84

Table 3 shows that mean vertebra count does not differ significantly between sexes, in four reasonably large groups of material of the same age-group, year-class, and locality. Sexual dimorphism in this character is rare in fish. Accordingly the sexes are combined in the material of other tables.

Only one comparison could be made between age-groups in the same year-class at the same locality (1939-40, Port Phillip). Sixty III-group specimens had mean 49.87 and Sx^2 14.934, and 269 IV-group fish had mean 49.83 and Sx^2 76.134, t being 0.53 and the difference non-significant. However, the possibility of significant variation between ages in other material could not be excluded, and comparisons between year-classes at the same locality were confined to specimens of the same age. The tests are summarized in Table 4.

TABLE 4

MEAN VERTEBRA NUMBERS COMPARED FOR YEAR-CLASSES IN HOMOGENEOUS MATERIAL

Material	1939-40			1940-41			1945-46			1946			1947			t
	N	*A.M.*	Sx^2	*N*	*A.M.*	Sx^2	*N*	*A.M.*	Sx^2	*N*	*A.M.*	Sx^2	*N*	*A.M.*	Sx^2	
Port Jackson — II-group										128	49.76	55.493	108	49,94	36.549	2.20
Port Phillip — III-group	60	49.87	14.934	133	49.80	33.520										0.90
Port Phillip — III-group	60	49.87	14.934				59	49.85	15.628							0.21
Port Phillip — III-group				133	49.80	33.520	59	49.85	15.628							0.63

Of the four comparisons in Table 4, one reveals a significant difference (of 0.18 vertebrae) in successive year-classes, the other comparisons being based on less plentiful material. Thus this type of variation is probably common and could explain the differences in sample means at individual localities and the irregular variation between localities, to the extent that such variation is significant. It follows that the locality means of Table 1, based on bulk unclassified vertebral counts, are not as reliable for stock analysis as would be a series based on counts of a single year-class. Actually it is only possible to make two comparisons between localities for a reasonably large material of the same year-class and age-group. These are summarized in Table 5.

Neither of these differences is significant. Thus the most reliable conclusion to be drawn from the entire study of vertebra numbers is that there is probably a single stock of pilchards on that part of the New South Wales coast from Port Jackson northwards. This is supplemented by the conclusions previously drawn from the data of Figure 2, that the fish occurring at Port Jackson, Twofold Bay, Lakes Entrance, Port Phillip Bay, Coffin Bay, and Queen Charlotte Sound probably all belong to different populations. The means for the first five localities show a trend with values diminishing north and west from Twofold Bay, which was less clearly indicated by the total assemblage of means in Table 1.

For this reason, and because of the size and variety of the material which the five means represent, the results of t-tests between them are acceptable as indications of stock differences. Some of these indications are supported by other evidence (see below).

(ii) *Scale Size.*—There is a regular trend in the mean size of certain scales of pilchards of the same length obtained from New South Wales (taken as a whole), Lakes Entrance, and Port Phillip Bay. The means are usually lowest in New South Wales and highest at Port Phillip, with intermediate values at Lakes Entrance, for fish of any given length (Blackburn 1950*c*). The scales in question are those on the ventral half of the subdorsal portion of the flank; they are measured from the middle of the basal line to the anterior apex.

TABLE 5

MEAN VERTEBRA NUMBER COMPARED FOR LOCALITIES IN HOMOGENEOUS MATERIAL

Material	Byron B.			Pt. Stephens			Bird I.			Pt. Jackson			t
	N	$A.M.$	Sx^2	N	$A.M.$	Sx^2	N	$A.M.$	Sx^2	N	$A.M.$	Sx^2	
1937 Class, II-group				90	49.82	61.156	75	49.61	53.788				1.60
1946 Class, II-group	99	49.63	69.173							128	49.76	55.493	1.31

(*c*) *Physiological Characters*

(i) *Growth Rate.*—The growth rate of pilchards was investigated in some detail, mainly from scale readings, in New South Wales and Victorian waters (Blackburn 1949, 1950*c*). The comparison is most conveniently made between the ranges of L_1, L_2, etc., i.e. the calculated standard fish-lengths at the times of formation of the successive annual rings. In Victorian fish a ring is formed at the conclusion of each year of life, but in New South Wales the first ring is formed when the fish is about $1\frac{1}{4}$ years old, the second at 2 years, the third at 3, etc. The L_n ranges, as published previously, are as follows:

	VICTORIA		NEW SOUTH WALES
L_1:	61-104 mm.	cf.	64-111 mm.
L_2:	85-127 mm.	cf.	100-143 mm.
L_3:	107-147 mm.	cf.	129-165 mm.
L_4:	123-165 mm.	cf.	151-181 mm.
L_5:	137-177 mm.		

The minimum value of L_2 in New South Wales probably ranges down to about 95 mm. (Blackburn 1950*c*, Section II (*d*) (iii)). There is insufficient information about the range of L_5 in New South Wales material, but specimens from 16.5 cm. (i.e. 165-169 mm.) to 19.0 cm. (i.e. 190-194 mm.) have been identified as five years old. The growth rate of Victorian pilchards is clearly much less than that of New South Wales fish, from 2 years of age onwards.

Much less scale material was available from other areas, and reliable L_n data were unobtainable because the fish-length/scale-length relationship could not be determined. However, several age determinations were made from scales collected on the south coast of Western Australia, and these showed that the growth rate in that area is probably not the same as that in either New South Wales or Victoria (Blackburn 1950*c*). Some three-year fish were as large as 16.0 cm., while the maximum size for this age in Victoria is only 14.5 cm. On the other hand some four-year fish were as small as 13.5 cm., as compared with a minimum of 15.0 in New South Wales.

The numbers of age determinations that could be made in other areas were even smaller (Blackburn 1950*c*). Those for South Australia could conform with either the Victorian or Western Australian scheme of growth rate, although not with that of New South Wales. The Tasmanian pilchards were mostly five years old, and their size range was very like that of similar fish in Victoria, but relatively few fish of that age have been identified in New South Wales. It is therefore probable, but not certain, that the growth rate in Tasmania is more like that in Victoria than in New South Wales.

These results support the more tentative conclusions reached from the study of spawning season variation. The autumn-to-spring spawners of New South Wales, the spring-summer spawners of Victoria, and the autumn-winter spawners of southern Western Australia have different growth rates and therefore represent substantially independent groups. The summer-autumn spawners of South Australia may belong to either or both of the two adjacent groups. The Tasmanian fish probably belong to the same main group as the Victorian.

(ii) *Age at First Maturity.*—At Lakes Entrance many pilchards are sexually mature at one year of age, and few fail to reach maturity at two years; but at Port Phillip few if any fish ripen at one year, and a significant percentage of two-year fish are still not mature (Blackburn 1950*c*). The position in New South Wales is broadly similar to that at Port Phillip (Blackburn 1949).

(*d*) *Fluctuations in Abundance*

A quantitative study was made of the availability of pilchards in surface waters at the optimum (winter) shoaling season in northern and southern New South Wales waters (Blackburn and Tubb 1950). The northern area, as rather arbitrarily recognized in that work, extended from the Queensland border south to, but not including, Port Jackson; the southern area comprised Port Jackson and all waters south to the Victorian border. The measure of annual relative availability was the percentage of days of observation at sea on which pilchard shoals were seen. This index fluctuated significantly over a period of four successive seasons (1939-1942) in the southern area, and it was shown that the changes were due to a succession of year-classes of widely varying numerical strength. It was therefore concluded that changes in the availability index indicated actual changes in abundance. In the northern area the fluctuations were not significant over the same period. This showed that the pilchards of the two areas belonged to two different populations, whose line of demarcation or overlap was probably in the neighbourhood of Port Jackson. The foregoing study of vertebra counts shows that it is to the south of Port Jackson, but probably not far south. It is certainly not as far south as Jervis Bay, because a great deal of the survey work from which the southern availability indices were calculated was done in that area. It can be shown from Table 1 that the mean number of vertebrae for 972 pilchards taken from Byron Bay to Port Jackson is 49.83, while the mean for 864 pilchards from Jervis Bay to Twofold Bay is 50.05. The difference is significant.

III. Conclusions and Remarks

The following conclusions are drawn regarding the presence and distribution of different groups in *Sardinops neopilchardus*:

(1) Three major groups, to which the fish of New South Wales, Victoria, and southern Western Australia respectively belong, are identifiable in Australian waters. The first (eastern) group consists of fish that spawn between autumn and spring, and have a relatively high growth rate; the second (south-eastern) group consists of spring and summer spawners with a relatively low growth rate; and the members of the third (south-western) group spawn in autumn and winter and grow at a rate probably intermediate between the other two. Pilchards of southern Queensland probably belong to the eastern group, as the spawning season there is a continuation of that in New South Wales. Those of Tasmania probably belong to the south-eastern group. The information on South Australian pilchards is too scanty for a clear decision as to whether they belong to the south-eastern or the south-western group or both. There is insufficient information from which to classify the fish of the west coast of Western Australia. The area of demarcation or overlap of the eastern and south-eastern groups is fairly sharply defined, being in the New South Wales-Victoria border region. Other evidence of discontinuity in this region is provided by the studies on vertebra number, scale size, and age at first maturity. These major groups are regarded as races, as there is insufficient evidence to call them subspecies.

(2) The eastern and south-eastern races are themselves not homogeneous, and the same might therefore apply to the south-western race. The eastern race consists of at least two largely independent populations, ranging respectively north and south along the New South Wales coast from a bounding or overlapping area between Port Jackson and Jervis Bay. The northern population ranges at least to Byron Bay. The evidence for these statements is obtained from studies on vertebra counts and abundance fluctuations.

(3) The south-eastern race consists of at least two populations, which include fish occurring at Lakes Entrance and Port Phillip Bay respectively, although nothing further is known about their geographical ranges. This is shown by differences in mean vertebra number, mean scale size, and age at first maturity in the material studied from these two localities.

(4) The fish occurring at Coffin Bay probably do not belong to the same population as those at Port Phillip Bay. The evidence is that of unclassified but presumably representative vertebra count data.

(5) The pilchards of Cook Strait, New Zealand, probably do not belong to the same population as any of the Australian fish. This is deduced from the fact that the mean vertebra number is relatively very high, and based on a reasonably large and representative number of counts. As few traces of pilchards have been found beyond the neritic zone on the Australian coasts, a high degree of geographical isolation between the Australian and New Zealand fish may be presumed.

It is of interest to compare the findings with those for the anchovy, *Engraulis australis,* which has a similar range in Australian waters. In that species there are also three major intraspecific groups (called subspecies), with subsidiary populations in each (Blackburn 1950*a*). The subspecies *E. a. australis* ranges along the eastern Australian coast as far south as Wagonga River, *E. a. antipodum* from Twofold Bay to Coffin Bay and through Tasmanian waters, and *E. a. fraseri* occurs in Western Australia. There are thus eastern and south-eastern groups of anchovies that are delimited like the corresponding groups of pilchards.

The foregoing conclusions have an important and, on the whole, a favourable bearing upon the prospects for the development of a significant pilchard fishery in Australia. At an early stage in this investigation it was noticed that the availability of pilchards tended to fluctuate, sometimes very significantly, from year to year in the same area, and it was felt that this might militate against the successful establishment of a pilchard industry, or of a tuna industry utilizing pilchards as live bait. The present study shows that there are several independent or quasi-independent populations (stocks) of pilchards whose individual range is of the order of hundreds rather than thousands of miles. This means that the years of relative abundance or scarcity will not necessarily be the same in all stocks or even in adjacent stocks, and it has actually been shown that they may be very different (see above). Thus, while an industry operating on catches from a restricted area would probably be affected by natural fluctuations (though perhaps to a less extent in some areas than others; cf. availability data for northern and southern New South Wales (Blackburn and Tubb 1950)), a firm with branch processing plants in two or more well-separated localities might find these local variations much less disturbing. Fast, far-ranging tuna clippers seeking pilchards for live bait would have the choice of different stocks for fishing at any particular season of the year, and if the fish seemed to be scarce in one area another could be tried with a greater expectation of success. This study gives some indications of the probable ranges of certain stocks.

IV. ACKNOWLEDGMENTS

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GROWTH AND HABITS OF THE SEA MULLET, *MUGIL DOBULA* GUNTHER, IN WESTERN AUSTRALIA

By J. M. THOMSON*

(*Manuscript received February* 6, 1951)

Summary

Morphologically and physiologically, the sea mullet of Western Australia seems to be identical with that of the eastern Australian coast. No raciation can be detected either within Western Australian waters or between the stocks of eastern and Western Australia. However, the mean growth rate varies from one estuary to another and from year to year within any particular river system. Growth is isometric and shows considerable individual variation though tending to a mean rate. Increase in length is seasonal, practically stopping in midwinter and reaching a peak in midsummer. The seasons of fish and scale growth are contemporaneous. The annuli form at the end of September or the beginning of October, when growth recommences after the winter cessation.

Mullet mature at a size of 31-35 cm. (12¼-13¾ in. length to caudal fin) at the end of their third year. The movement of mullet from the fishing grounds as they increase in size leads to an incomplete sampling of the population so that Petersen's method of age determination is inapplicable owing to the apparent nonprogression of the modes. Of 7110 mullet tagged, only 97 or 1.35 per cent. were returned. The return for separate tagging operations varied from nil to 25 per cent. and according to localities from nil to 16 per cent. Only three fish were retaken outside the rivers in which they were tagged. These showed a northerly movement. Inside the rivers the young fish spread out over the estuary and into the fresh water; but the older age-groups remain in the slightly brackish or fresh water except during the migration season, when they pass through the saline estuaries on the way to the sea.

I. INTRODUCTION

The adequate management of any fishery resource can only follow a thorough knowledge of the biology of the species of fish concerned. Certain conclusions concerning the Australian sea mullet (*Mugil dobula* Günther) have been published by Kesteven (1942). His data referred mostly to fish from the eastern seaboard of Australia. Management reforms in the Western Australian fishery have been recommended (Kesteven 1941) largely on conclusions derived from the study of the biology of the eastern stocks. As these are generally considered not to intermingle with the Western Australian mullet it is desirable to determine whether the biology of the eastern and western fish is identical. The most important features to be taken into account are the rate of increase in size and in weight, the size at maturity, and the habitat preferences of the fish at different ages.

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II. Collection of Data

Samples of mullet were obtained from the Perth fish markets and from experimental hauls made in various mullet waters. The former source was the only one available for regular sampling throughout the year. Centralized fish marketing is not enforced in Western Australia and fish from only two sources, namely Peel Inlet and Shark Bay (Fig. 1), regularly passed through the markets at the time the study was made. Fortunately these are typical of the waters supplying small and large fish respectively so that representative sampling was permitted. The

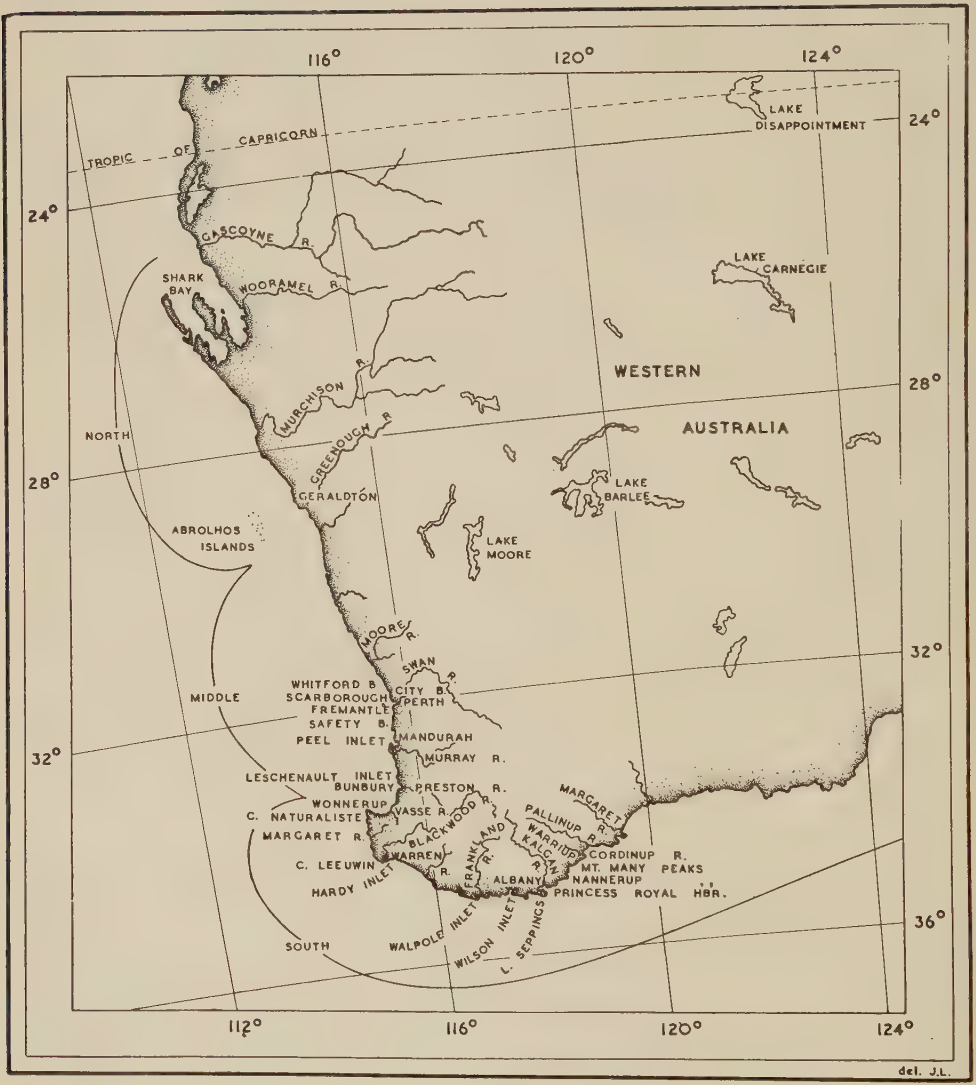

Fig. 1.—South-western Australia.

bulk of the sampling consists of length measurements with subsampling for weight and scale samples for age determination. Over 60,000 fish

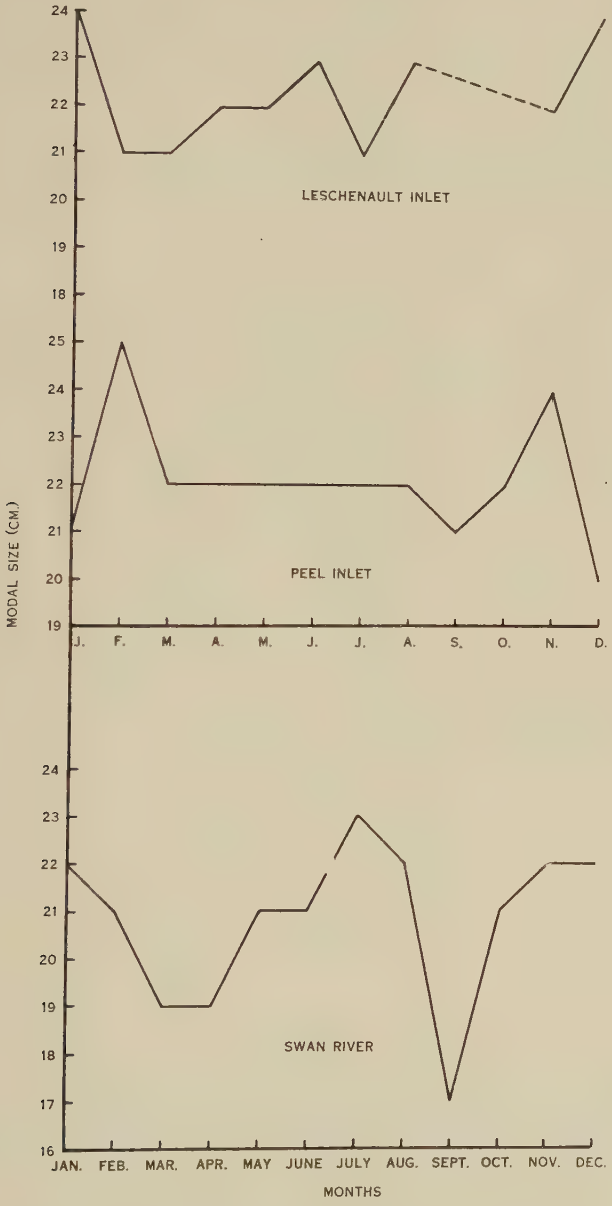

Fig. 2.—Modal size groups taken in commercial fishing in the main western estuaries.

were measured, 2,200 were weighed, and 2,000 scale samples were taken for age and growth determinations.

III. RATE OF GROWTH

(a) *Lineal Growth*

Direct evidence of growth rate may be obtained from measurements of tagged fish at the time of tagging and at recapture. Such evidence is meagre for mullet in Western Australia and serves rather to confirm findings by other methods rather than to establish a satisfactory independent body of data (Appendix V).

Two indirect methods of the determination of size at various ages have been utilized, namely Petersen's method and the scale-reading technique.

(i) *Length Frequency Studies*

Petersen's method of interpreting the modes of a graph of size distribution as the modal lengths of successive year-groups has been used successfully where several age-classes occur in the fishery. It is difficult to obtain more than one or two year-classes from any one area in Western Australia owing to the nature of the dispersion of the year-classes (Thomson 1950), and no progression of the modes can be detected in the age distribution of the three main western estuaries (Fig. 2).

However, a reasonably clear picture is given by the distributions for Hardy Inlet and Shark Bay (Fig. 3). For instance, five distinct modes can be made out in June. These can be interpreted as successive age-groups. As June is the end of the spawning period, these figures may be taken as the lengths attained at the end of succeeding years. Thus, assuming the first peak to represent the length attained at the end of the first year the modal sizes in Table 1 are obtained.

TABLE 1

MODAL SIZES OF SEA MULLET

Age in Years	Modal Size (cm.)
1	15
2	24
3	34
4	38
5	42

Growth through the year may be traced by the progression of the modes from month to month. The 15 cm. mode in June can be traced from one at 12 cm. in February, followed through to a size of 20 cm. in the following November, and progresses to become the 24 cm. mode of the next winter. Similarly each size-group can be traced during its seasonal growth. It is notable that growth is at a minimum, if not altogether halted, during the winter months from June to September. The progression of the modes indicates that the rate of growth is greatest over the midsummer months.

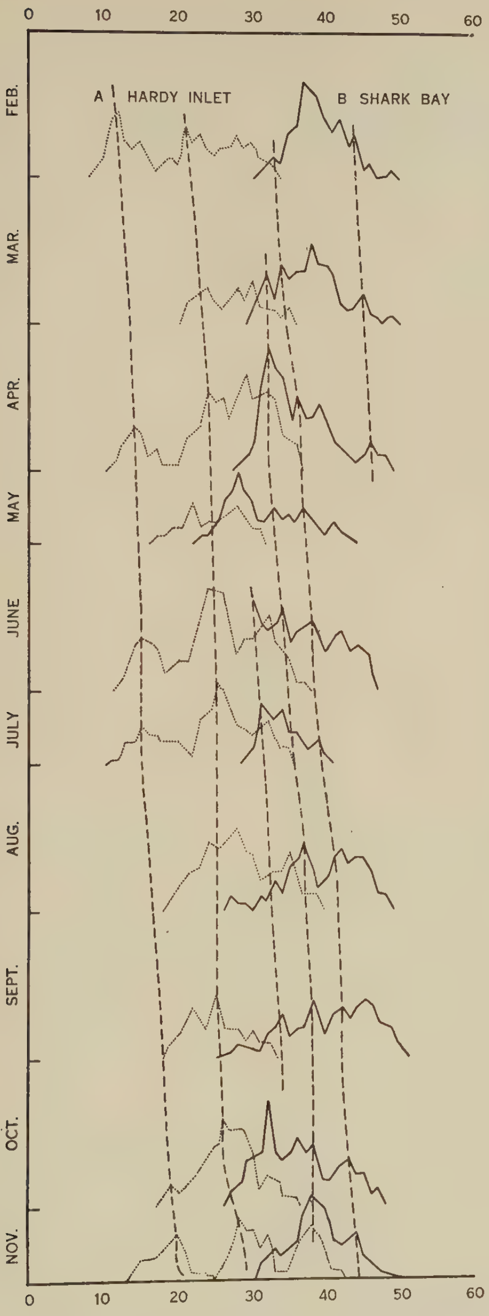

Fig. 3.—Length frequency distributions, Hardy Inlet and Shark Bay, showing progression of the modes.

However, the modal progressions are not always clear. Some modes fail to appear in certain months; for instance, the 25 cm. mode in the

June curve cannot be detected in that for July. Presumably this indicates non-availability of this particular size-group during that month, probably as a result of migration to unfished waters, or possibly owing to the inability of the fishermen to obtain them in their usual haunts as a result of floods, stormy weather, or other environmental disturbance.

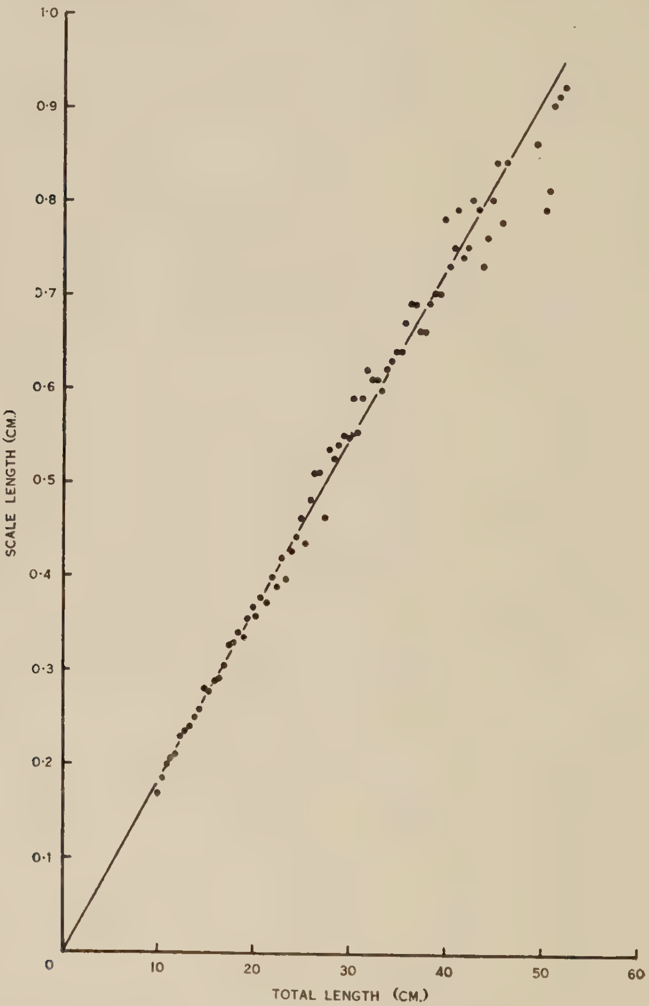

Fig. 4.—Relationship of scale size to total length of fish.

At other times, apparently spurious peaks confuse the interpretation of the size distributions, as for example in the larger size ranges for October. In such cases the correct modal peaks may be ascertained from the rate of growth in preceding and subsequent months. The spurious peaks appear to be due to inadequate sampling rather than to the movement into the area concerned of a stock with different growth characteristics. If the latter were the case there should be some persistence of the extra modes, but this does not occur.

(ii) *Scale-Reading Determinations*

The usefulness of the scale-reading methods with the sea mullet has been discussed by Kesteven (1942). The validity of the scale-reading method for the estimation of age and growth rests on the assumptions that the scale size bears a constant relationship to the length of the fish, and that the observed breaks (annuli) are formed annually and therefore provide a record of the age of the fish.

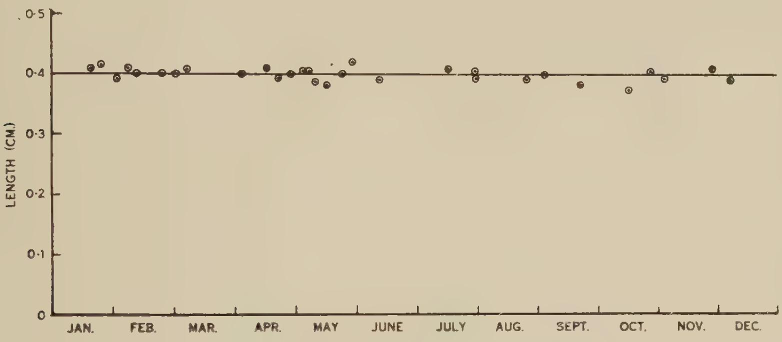

Fig. 5.—The scale size of fish 24 cm., 3 C.F., taken at various times of year.

That the former assumption is valid is verified by the regression line of scale-length on fish-length (Fig. 4). There is an increased scattering in the data for fish of large size, but this is due to the relatively few measurements available, and is uniform about the mean line. There does not appear to be any change in the relative growth of scales and body such as Huntsman (1918) and Duff (1929) found in the cod, and Thompson (1923) found in the haddock. Duff (1929) also found that the seasonal growth of scale and fish did not correspond. However, no seasonal discrepancy can be detected in the mullet. The mean values of scale size at different times of the year for fish of a particular length show a normal scatter about an average value (Fig. 5) and do not fit a sine curve such as Duff found for the cod.

(1) *Annual Growth.*—The mean lengths to the caudal fin (L.C.F.) attained each year at the time of formation of the annuli are 14.00, 24.08, 33.06, 40.52, 46.74, 50.76, and 55.5 cm. respectively for the first, second, third, etc., years (Fig. 6*A*). The first three figures do not differ very much from those found by the Petersen method. However, there does appear to be some discrepancy in the fourth and fifth year figures. Scale readings for Shark Bay mullet give a fourth year length of 40.27, which is not far from the mean for fish from all Western Australian waters. No scales from a V+ fish from Shark Bay are available for checking.

The annual growth increments are shown in Figure 6*B*. They become progressively smaller with age, but although the growth rate slows there has been no approach to cessation of growth in the oldest groups so far captured.

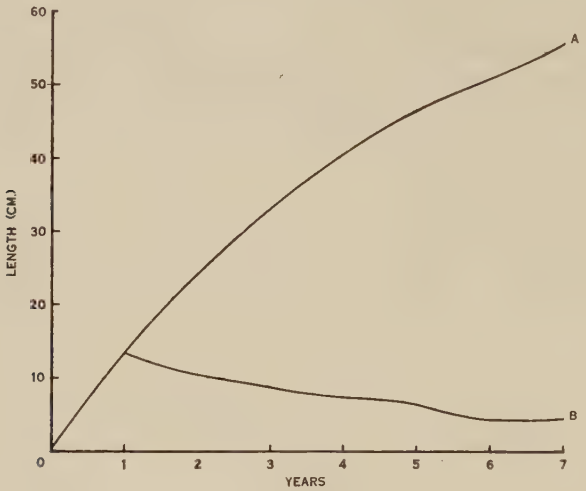

Fig. 6.—Mean growth of mullet (line *A*) showing the annual increments (line *B*).

Contrary to the evidence of Dannevig (1902), Kesteven (1942) found no significant difference between the growth rate of males and females. The data in Table 2 for 113 male and 67 female mullet from the same source (Shark Bay) in Western Australia support Kesteven's contention. These mean values show slightly higher figures for the females but the difference is small and not significant.

TABLE 2

GROWTH OF MALES AND FEMALES

Age (years) Sex	I—	II—	III—	IV—	V—
Male	13.01	23.8	32.6	39.43	43.2
Female	13.27	24.38	34.63	40.82	44.01

(2) *Seasonal Growth.*—Scale and fish growth are contemporaneous (Fig. 4). Therefore, if growth is seasonal and not uniform over the year, the rate of growth at different times of the year may be estimated from a study of the formation of marginal increments on scales taken in different seasons. The marginal increments are the portion of the scale secreted since the last annulus was formed. The mean monthly increments as shown by scale reading are shown in Table 3.

From the values for growth from the end of the first year to the end of the second year, Figure 7 has been constructed. Similar curves can be constructed for older fish. It is evident that growth is greatest between November and February and that it ceases altogether between June and September for about 2½ months.

TABLE 3

MEAN MONTHLY INCREMENTS

(cm.)

Region	Age	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	1					11.3		12.3					
	2					8.4			6.4	0.7			
North	3		5.6		7.8		5.3		4.4	0.3	2.7	4.7	
	4		3.1				4.4		3.2	1.0	4.2		
	5												
	1		8.2	9.0	10.2	11.1	10.9	11.0	10.7		9.9 1.0	1.7	
	2		5.4	5.8	8.0		10.5		9.5		0.7	1.4	
Middle	3		3.1	4.6	4.0	4.0			6.5				
	4				2.9				3.0				
	5												
	1	5.5	9.1	10.7		11.0	12.9			10.8			
	2	4.9	5.8	8.3		8.5			8.8	7.8			2.0
South	3	1.8	3.5	3.5		4.5	7.0	8.5					1.7
	4		3.5	3.4	3.1	2.4	2.3			3.0			
	5		3.1	3.5	2.6	2.7				3.2			
	6				2.4					1.5			
	1	5.5	8.6	9.8	10.2	11.1	11.9	11.7	10.7	10.8	9.9 1.0	1.7	
	2	4.9	5.6	7.1	8.0	8.4	10.5	8.5	8.3	7.8 0.7	0.7	1.4	2.0
Mean all	3	1.8	4.1	4.1	5.5		6.1		5.5	3.7 0.3	2.7	4.7	1.7
regions	4		3.3	3.4	3.0		3.3		3.1	3.0 1.0	4.2		
	5		3.1	3.5	2.6					3.2			
	6				2.4					1.5	2.1		

The curve is similar to that figured by Hjort (1914) for seasonal growth of the herring. But with the herring the cessation of growth extended over a much longer period, doubtless in correlation with the longer period of low temperatures in northern European waters.

That seasonal growth is associated with temperature (probably indirectly) is generally assumed (Ancona 1937; Bily 1938). In Figure 8 the increment in each month is plotted below the curve of the temperature over a period of 12 months in the upper estuarine waters of the river. The agreement is fairly close. It would appear that, at least in these waters, the growth of mullet ceases as the temperature drops to 18° or

16°C., to commence again when the temperature rises to that level once more.

(3) *Age and Time of Formation of the Annulus.*—As the "break" or annulus in the circuli of the scale is used as the criterion of age it is of some importance that the time of its formation be known. Table 3 reveals that the annulus is formed in all age-groups at the end of September or beginning of October. It appears a little earlier in the more northern waters where temperatures rise sooner. The small increments shown for September in more northern waters were obtained from fish netted on September 30. In the west coast rivers, two types of second year (I+) fish could be distinguished by the second week in October. One of these groups showed an increment of 1.0 cm., the other an increment of 9.9 cm. By November, scales displaying small marginal increments only were found. During October, the third year fish (II+) in some cases exhibited the beginning of the annulus on their edges while others showed a definite margin (mean increment of 0.7 cm.). There appears to be some individual variation in the critical temperature level for the stimulation of growth. There is lack of data from the crucial period in southern waters.

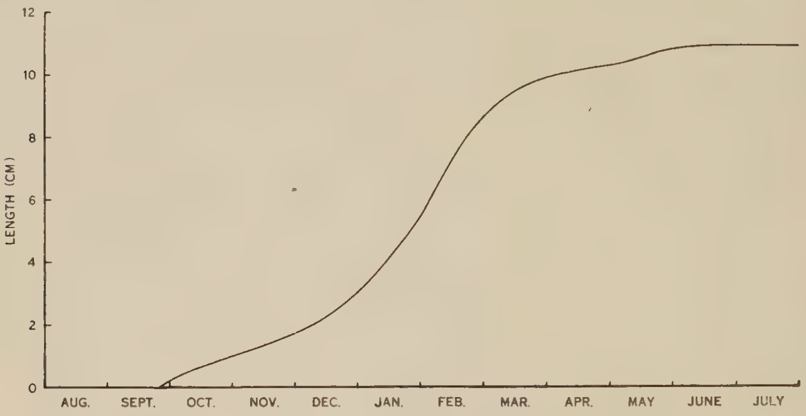

Fig. 7.—Seasonal growth of second year mullet.

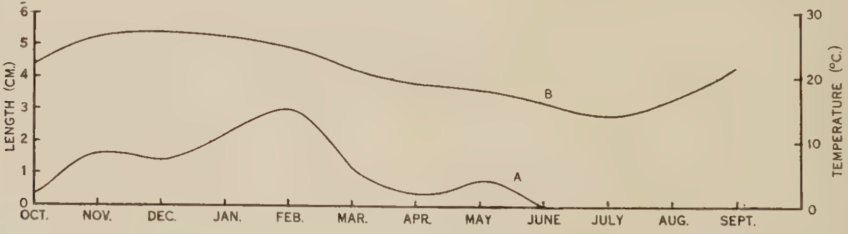

Fig. 8.—Comparison of monthly growth increments (line *A*) with temperature (line *B*).

TABLE 4

MEAN CALCULATED INTERMEDIATE LENGTHS (CM.), ALL LOCALITIES, SHOWING NUMBER OF FISH SAMPLED

Locality	Intermediate Lengths													
	L_1	No.	L_2	No.	L_3	No.	L_4	No.	L_5	No.	L_6	No.	L_7	No.
Shark Bay	13.84	228	23.77	133	33.23	43	40.27	13						
Abrolhos Is.	15.50	15	25.50	14	33.41	14		4						
Geraldton	15.62	32	25.09	12	34.50	12	40.75	17						
Total north	14.03	275	24.04	155	33.49	69	40.38							
Whitford's Beach	14.40	98	24.30	59	34.10	10								
City Beach	14.40	11	25.50	4	37.50	1								
Scarborough	12.50	8												
Swan River	13.80	135	24.50	1										
Safety Bay	13.00	10												
Peel Inlet	13.00	397	23.40	133	34.10	16								
Leschenault Inlet	14.95	20	24.00	8	32.50	1								
Busselton	13.85	21	23.77	11	34.50	2								
Unspecified locality	13.41	1	23.80	2	35.10	2								
Total middle	13.40	701	23.82	218	34.75	32								
Margaret R.	15.92	75	25.29	70	33.74	70	40.44	66	46.74	45	50.93	21	55.50	3
Hardy Inlet	14.63	123	25.11	68	32.39	35								
Frankland R.	12.25	51	21.96	43	30.83	3								
Wilson's Inlet	14.96	172	23.96	136	33.14	74	40.08	26	42.36	7	49.00	2		
Albany	12.86	118	24.05	101	34.50	23	41.06	25	47.70	15				
L. Seppings	15.09	61	24.00	26	31.70	5								
Nannerup	12.01	41	23.70	22	36.75	4	43.00	2						
L. Gardner	14.50	12	24.95	11										
Pallinup	14.00	17	23.59	22	35.02	21	41.50	1						
Total south	14.47	670	24.20	499	33.50	235	40.54	120	46.74	67	50.76	23	55.50	3
Mean W.A.	14.00	1646	24.08	872	33.60	336	40.52	137	46.74	67	50.76	23	55.50	3
Mean eastern Australia	14.86	1639	23.07	1203	31.73	621	39.70	207	47.67	44	53.73	20		

Growth ceases during July and August. The annulus thus becomes apparent when growth recommences after a period of cessation. Presumably additional (false) annuli (Kesteven 1942) are formed when growth ceases at periods other than the winter quiescence whether owing to accident, illness, or environmental effect. These additional annuli are not spawning effects as spawning occurs in early winter when growth has ceased, nor can these annuli be interpreted solely as spawning marks because the immature, non-spawning fish show exactly similar annuli. Whether omitted annuli indicate that the fish did not stop growing in a particular winter is problematical.

TABLE 5

ANNUAL INCREMENTS IN GROWTH (CM.)

Locality	L_1	i_1	i_2	i_3	i_4	i_5	i_6
Shark Bay	13.84	9.93	9.46	7.04			
Abrolhos Is.	15.50	10.00	7.91				
Geraldton	15.62	9.47	9.41	6.25			
Whitford's Beach	14.40	9.90	9.80				
City Beach	14.40	11.10	12.00				
Swan River	12.50	10.70					
Peel Inlet	13.00	10.40	10.70				
Leschenault Inlet	14.95	9.05	8.50				
Busselton	13.85	9.92	10.73				
Hardy Inlet	14.03	10.48	7.28				
Frankland R.	12.25	9.71	8.87				
Wilson's Inlet	14.96	9.00	9.18	6.94	2.26	6.60	
Albany	12.86	11.19	10.45	6.56	6.64		
L. Seppings	15.09	8.91	7.70				
Nannerup	12.01	9.69	13.05	6.25			
L. Gardner	14.50	10.45					
Pallinup	14.00	9.59	11.43	6.48			
Margaret R.	15.92	9.37	8.45	6.70	6.30	4.19	

Spawning occurs in May or June, but the annuli do not become evident until September or October. Thus the first annulus does not become evident until an age of approximately 16 months instead of 12, and similarly all the annuli appear not at 1, 2, 3, etc., years but at $1\frac{1}{4}$, $2\frac{1}{4}$, $3\frac{1}{4}$, etc. However, as growth ceases or is minimal during these four months the lengths obtained by scale readings are good approximations to the annual growth.

Jacot (1920) interpreted the annuli as migration marks but, as the tagging indicates (Section IV (*b*)) that many fish do not travel, the explanation of growth cessation is more plausible.

(4) *Local Variation in Growth Rate.*—There is some variation in growth according to locality (Table 4). The difference between the highest and lowest values for the size at the end of the first year's growth does not seem considerable in absolute figures (3.9 cm.) but this is a 25 per

cent. difference in length at that age. This proportional difference drops continually with age although the absolute difference remains much the same, but there is no continuing trend of growth at a slow or fast rate in any one locality. The localities that produced fish exhibiting the slowest growth during their first year do not necessarily show the lowest increments in the second year (Table 5), nor do such fish tend uniformly to have second year increments greater than those of fish that grew faster in the first year as demanded by the theory of compensatory growth (Watkin 1927).

Any differences in the growth of fishes from particular localities cannot be ascribed to some continuing differences peculiar to the localities themselves, but to ecological factors that vary irregularly from time to time and from place to place. There are no data to indicate what factors are involved, though it is probable that abundance of food, which itself depends upon other factors, plays a large part in producing the variations. However, there are not the distinct differences in growth that have been demonstrated for plaice in the North Sea (Petersen 1922).

TABLE 6

RANGE IN SIZE AT END OF FIRST YEAR AS INDICATED BY SCALE READING

Size (cm.)	Swan R.	Peel Inlet	Margaret R.	Wilson's Inlet	Hardy Inlet
8		2		2	1
9	1	19		5	7
10	1	42		17	10
11	11	98		23	7
12	10	75		14	23
13	16	38	4	23	20
14	20	53	16	32	21
15	14	35	15	20	29
16	5	20	12	18	17
17	2	8	12	20	5
18	3	9	5	16	6
19	1	2	6	2	4
20			2	2	1

Differences in local spawning time could also influence the size reached during the first year. Even in the one estuary there may be a considerable range in the length attained by the mullet at the end of the first year (Table 6), suggesting that the spawning period is prolonged over more than one month, or that large individual differences in growth rate occur.

The factors responsible for the differences in growth rate of fish in one estuary as compared with that in another doubtless operate also to produce fluctuations within any one estuary from year to year (Table 7).

(5) *Proportional Growth.*—The growth of various body portions is isometric, as is shown by Figure 9 and borne out by the indices set out

in Appendix I. Although the general trend of the regression lines is uniform, a not inconsiderable scatter is shown by the sample ranges in Appendix I, thus indicating a degree of individual variation in the relative size of parts of the body.

(6) *Individual Growth.*—The growth data presented are derived from the means of group samples and, although regular, represent only the general tendency of growth for the stock as a whole. Gray (1929) warned that the use of means is likely to overminimize natural variation. Davenport (1934) showed that curves of growth compiled from mass statistics may completely obscure features of the individual growth curve owing to superimposed curves of distribution. Richards (1935) also pointed out that small differences in growth rate or method of growth may be swallowed up in the general trend.

TABLE 7

FLUCTUATION IN MEAN LENGTH (CM.) ATTAINED BY FIRST YEAR FISH IN VARIOUS YEARS

Year	Wilson's Inlet	Hardy Inlet	Peel Inlet
1944			11.4
1943	11.7	14.8	14.3
1940		15.6	12.8
1939	14.5	14.8	13.1
1938	15.2	13.9	14.1
1937	13.8	14.6	14.7
1936	14.0		

The individual growth curves obtained by reading scales from selected fish are shown in Figure 10. Fish *E* and *G* parallel the curve of mean growth but the others show various trends away from the norm. Any tendency to diverge from the mean growth rate is not continued beyond one year and the tendency during the following season is to return towards the mean (Fish *F*) or at least settle down at the same rate as the mean though at a different level of absolute size (Fish *A*, *B*, *C*, *D*). There thus seems to be some physiological mechanism, presumably genetic in origin, which tends to keep fish of the one species growing at approximately the same rate. To some extent this seems to confirm Watkin's (1927) theory of compensatory growth, though the tendency seems to be not so much towards a common absolute size but towards a common rate of growth.

(*b*) *Increase in Weight*

The rate at which weight increases becomes steadily greater during the first two years of life but during the third year a constant mean rate of increase is attained, so that after reaching maturity at the end of the third year the rate of increase in weight is uniform (Fig. 11). However, the weight-length curves for different bodies of water are not identical.

The two curves in Figure 11 are those of the extreme cases, the curves for fish from other localities falling between the two.

No consistent differences are apparent between the male and female length-weight ratios (Table 8).

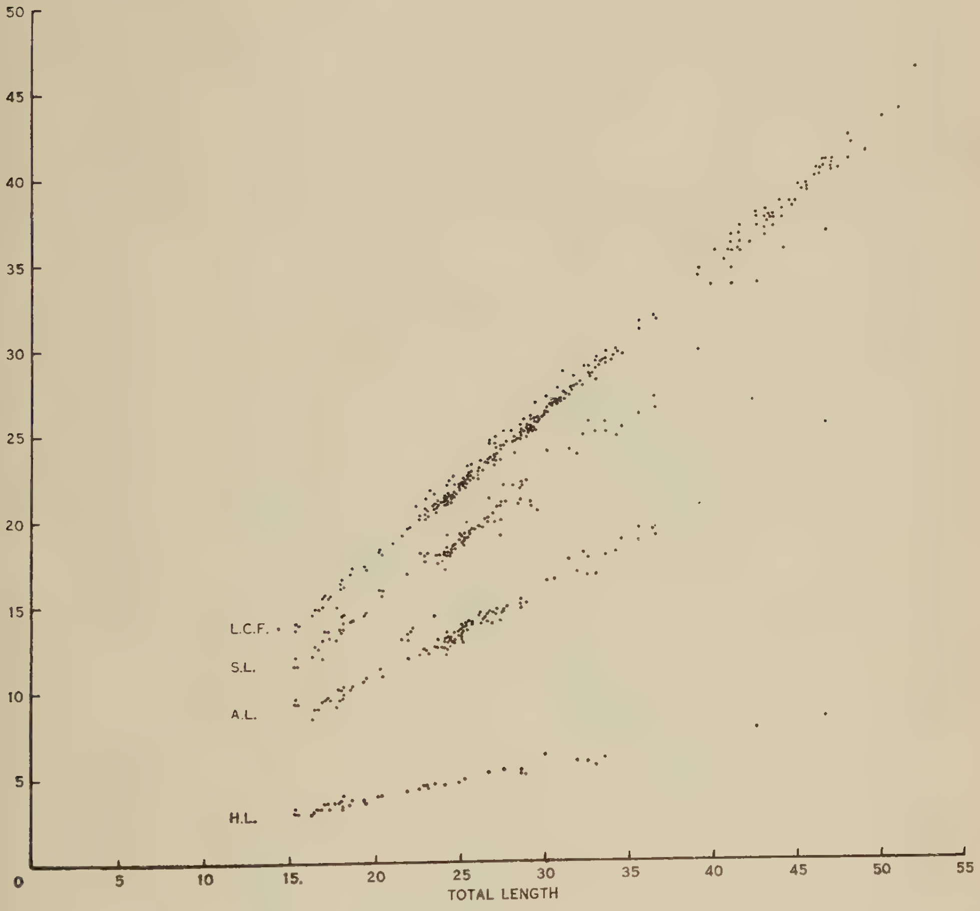

Fig. 9.—Relationship between total length and parts of the body.

The condition factor.—A much-used condition factor is the ponderal index K derived from the relationship $K = W/0.01L^3$, where W is the weight (g.) and L the length (cm.) (Hile 1936). This is based on the conception that the cube of the length has a constant mathematical relationship with the volume of the fish, so that K becomes a measure of the weight per unit of volume. This relationship holds only if growth is isometric. Clark (1928) and Hickling (1930) found the relationship to hold only between certain limits. Keys (1928) and Hickling (1930) found more useful the general relationship $C = W/0.1L^n$, where n is 3 only if growth is isometric. This was developed by Hart *et al.* (1940) who considered the use of *C* preferable for assessing seasonal variations within one population, but used *K* for comparing populations. However, the present study confirms Kesteven's finding that growth is isometric and that *C* approximates to *K*.

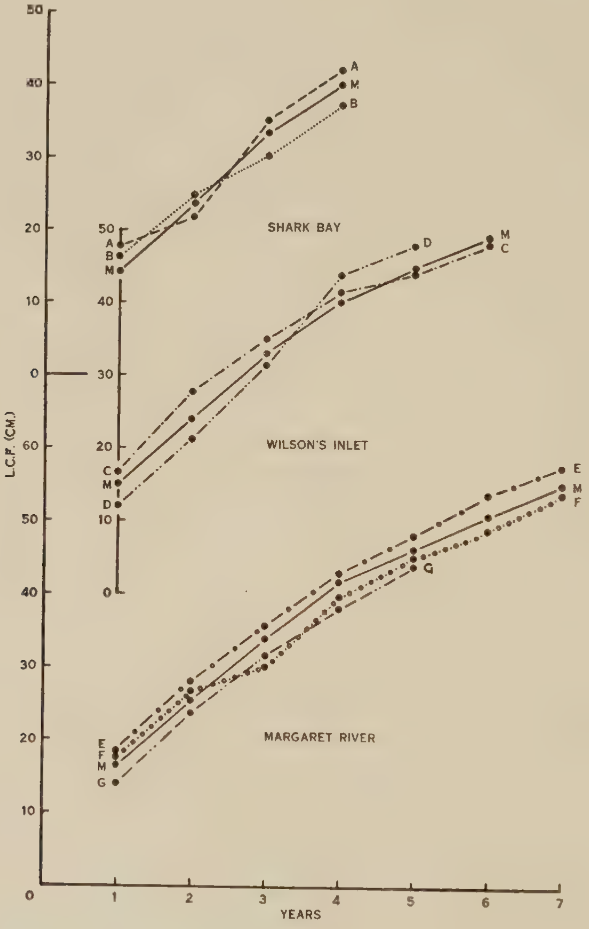

Fig. 10.—Growth curves of individual fish *A-G*. *M* is the mean growth rate in the particular locality.

Ancona (1937) pointed out that the condition factors will vary with months and seasons, state of nutrition, gonad maturation, and possibly with age. According to Ricker and Merriman (1945) the length-weight relationship can even vary with the time of day, and marked differences can be found in populations of the same species taken from different waters. This last factor applies particularly to the sea mullet, which passes freely through the estuaries into quite fresh water, for the resulting osmotic changes must lead to alteration in the weight-length relationship .

In Figure 12 are shown the monthly trends of *K* during a single year (1947) for fish from two bodies of water of different type and containing different age-groups. Peel Inlet is an enclosed inlet or marine-dominated estuary where immature fish (18-24 cm. L.C.F.) form the bulk of the commercial catch. The mean condition factor of these fish remains fairly constant throughout the year, dropping slightly in winter, possibly as a consequence of the scarcity of food, and rising slightly again in early summer. The reading for June is abnormal as only one large 40 cm. fish with mature gonads was available for examination in that month.

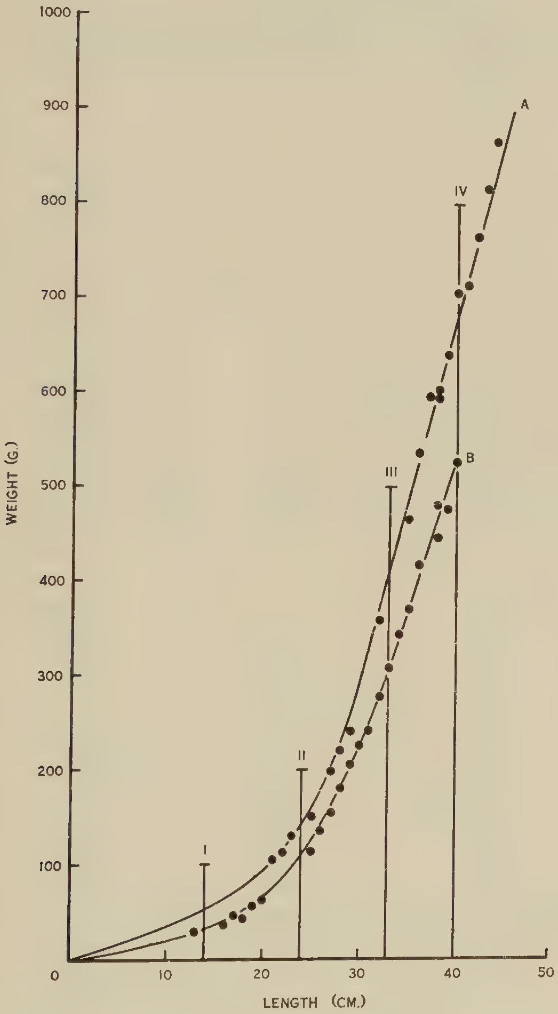

Fig. 11.—The length-weight relationship of mullet from Margaret River (*A*) and Shark Bay (*B*).

The second type of water is that of the ocean beaches such as are typified by Shark Bay fish, which are mature and between 34 and 41 cm. L.C.F. In these the trend of the condition factor is quite different, being high in summer but dropping sharply in midwinter, presumably as the result of spawning. A gradual recovery is shown later. No records are available for December and January as the prevailing stormy weather prevented fishing in Shark Bay during those months.

TABLE 8

LENGTH-WEIGHT RELATIONSHIP

Length (cm.)	Male Wt. (oz.)	Female Wt. (oz.)	Unsexed Wt. (oz.)	Total Wt. (oz.)
12			0.75	0.75
13			0.90	0.90
14			1.01	1.01
15			1.25	1.25
16			1.66	1.66
17			1.59	1.59
18			1.76	1.76
19			2.36	2.36
20			2.64	2.64
21	4.75		3.27	3.37
22			3.89	3.89
23			4.56	4.56
24	4.50		4.92	4.91
25	4.90	5.79	5.09	5.21
26	6.41	5.50	5.49	5.56
27			6.00	6.00
28	6.83		6.65	6.67
29	7.95		7.30	7.40
30	8.77	8.25	8.20	8.32
31	9.45	9.32	9.25	9.31
32	10.55	10.50	9.98	10.43
33	11.37	12.90	11.25	11.50
34	14.00	14.50	12.30	12.62
35	15.16	16.50	13.35	13.96
36	18.00	15.72	14.83	15.58
37	17.50	17.50	17.20	17.41
38	20.00	19.67	17.76	19.34
39	23.50	22.80	21.70	21.96
40	24.20	25.30	23.00	24.10
41	25.50	26.10	27.00	26.40
42			27.00	27.00
43			29.00	29.00
44	29.00	31.00	32.25	30.60
46	30.70	30.50	31.10	30.60

The condition factor level is not the same from one season to another. The mean value of *K* for fish from Peel Inlet taken in April in several years varied thus:

1939	1940	1941	1945	1947
1.05	1.02	0.97	1.06	1.06

Although the means show a consistent trend at any time the range of the *K* distribution is considerable. This is shown graphically in Figure 13 for fish taken in a single haul from Peel Inlet in April 1940. The presence of more than one mode is interesting. No correlation could be demonstrated with sex or other factors. However, at this time of year the mullet are moving downstream into the lower estuaries on the start of the spawning migration (adult fish) or in order to avoid floods (younger age-classes). It is suggested that the school sampled could have been a composite one including fish originating from more than one of the three rivers entering Peel Inlet. Thus various fish would have had different histories, resulting in different weights per unit of volume.

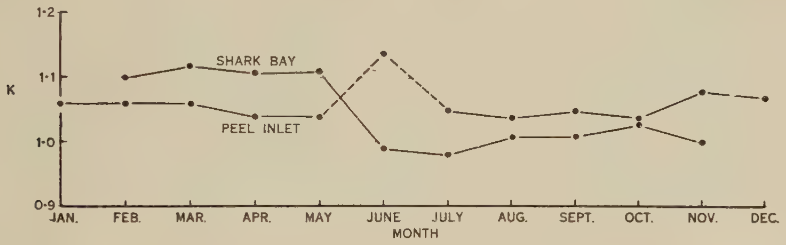

Fig. 12.—Monthly trends of the ponderal index *K*, illustrating difference in mature (Shark Bay) and immature (Peel Inlet) fish.

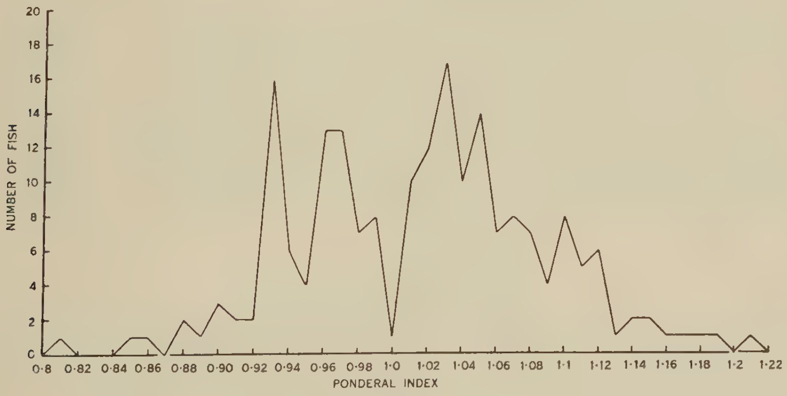

Fig. 13.—Distribution of ponderal index of mullet taken in a single haul, Peel Inlet, April 1940.

No gradation in the values of *K* can be distinguished for differences in latitude. An interesting problem is presented by the occurrence of distinct differences of K for two year-classes sampled simultaneously at Mt. Many Peaks estuary. Fifty-five fish with a mean L.C.F. of 26.1 cm. had a mean K of 0.96 (range 0.80-1.13); while 31 fish with a mean size of 11.3 cm. had a mean K of 1.36 (range 0.93-1.73). The unusually high values for K for the latter group may indicate that the ponderal index ratio does not hold for smaller fish. These were the smallest fish sampled. However, the next smallest group of fish (24 from Swan R.; L.C.F. 16 cm., mean K 0.98) does not show an intergrade between the 11 cm. fish and those still larger.

Possibly therefore, the differences in the indices for the two age-groups are due to causes other than size. Possible explanations include:

(*a*) The migration of one year-class from another estuary;
(*b*) Food available to one class is not suitable for the other;
(*c*) The two groups may differ genetically in weight-length ratio;
(*d*) Differences in gonad development may occur.

(*c*) *Maturity*

The gonad stages of 135 male and 192 female mullet over 25 cm. in length were examined. Ripening of the gonads first commences in fish about 27 cm. long (L.C.F.) and is completed at a length of 31 cm. However, spent gonads have not been observed in males smaller than 32 cm. or females smaller than 35 cm.

Ripe and spent gonads have been found in mullet from the southern part of Western Australia from May to September (Table 9), on the south-western coast from April to June, and in the north from March to September. However, in no case is the information really complete, but it is sufficient to show that spawning takes place over several months, which would explain the fairly wide range in the length attained at the time of formation of the first annulus.

IV. HABITS

(*a*) *Feeding*

In the lower estuaries, the sea mullet feeds on detritus, sucking in the accumulations, which are then strained in the pharynx (Günther 1861) so that only the finer elements enter the stomach, where the organic matter is digested. Not only detritus but also diatoms and the other minute constituents of the fauna and flora are ingested. There seems to be a limit to the size of the object which the mullet will swallow. Thus they do not swallow very small molluscs, although yellow-eye mullet (*Aldrichetta forsteri*) feeding side by side with them do so. In the fresh waters mullet depend to some extent on the green algae, fish from such waters usually having the stomach crammed with fine algal filaments.

According to Kesteven (1942), travelling fish are almost invariably empty-gutted. Fish from Shark Bay that are in roe conform with this observation but at other times of the year the gut contains material, principally algal matter.

TABLE 9

SEASON OF GONAD MATURATION

Section	Gonad Stage	I		II		III		IV		V		VI		VII		VIII		Total
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
	March															1		1
	May	26	46		2													74
North	June										1							1
	September	6	8	1	3						2					1		21
	October		1		1												4	6
	November																2	2
	January	39	23	5	10		2											79
	February	7	6			3												16
	March							1										1
	April	14	14	9	20		3	1	3	6	25	27	2	1		1	2	128
Middle	May	3	1	5	8		1				1							19
	June	3	4	1							4		2			1	2	17
	July		1		1			1										3
	August	24	15	1	5	8	15				1							69
	December	2	1		2													5
	February	4	1															5
	March			2		2					2							6
	April	3	4								2	1						10
	May	6		2	3	4					3	1					7	26
South	June	3		2	3	1										1	3	13
	July	4	7						1		4	3	1					20
	August	9	11		4	3	10											37
	September	15	12	4	8	2	4				1						1	47
	October		1															1
	Total	168	156	32	70	23	35	3	4	6	46	32	5	1		5	21	607

(*b*) *Movements of Mullet*

Reference has been made to the fact that at various times sea mullet may be found in fresh water, the estuaries, or the sea. Their movements are thus of both biological and commercial interest. In most Western Australian rivers the freshwater zone is of very limited extent and flow generally ceases during the dry summer months (Thomson 1950). This places greater emphasis on the estuarine and sea habitats than in eastern Australia.

The movement of mullet of various ages can be studied in two ways, firstly and most directly by tagging experiments, and secondly by examination of the nature of the population in different waters.

(i) *Tagging Experiments.*—The tag used in the Western Australian mullet tests was a simple opercular tag, marked C.S.I.R. on one arm and with a serial number on the other. The fish were measured when released.

In Western Australia, 7110 sea mullet have been tagged, mostly between November 1946 and January 1949. Of these only 97 or 1.36 per cent. were returned (Appendix II). The success of any tagging experiment depends to some extent upon the cooperation of the fishermen and market operatives in returning the tags when discovered. The percentage return varied in different estuaries but the figures are probably an index of cooperation rather than a measure of fishing intensity. Amongst Swan River fishermen in particular there was an often-expressed fear that the Division's activities would lead to unwelcome restrictions.

The percentage return from separate tagging operations varied from nil to 25 per cent., and, according to localities, from nil to 16 per cent. The period of freedom of the tagged fish varied from 1 to 1102 days, with a mean value of 88 days (Appendix III).

Only three of the 96 tagged fish returned had left the river system in which they were tagged. One of these (Tag C1830—Peel Inlet) had not moved far, being taken on the sea beach just outside the Peel Inlet bar. The second, also tagged in Peel Inlet (Tag A4204), was taken 310 days later in the Swan River, which is the next water system north of Peel Inlet, the distance being about 50 miles by water from tagging point to place of recapture. The third was tagged at the mouth of the Collie River in Leschenault Inlet and was taken 485 days later on Geraldton Beach, some 350 miles to the north.

It should be noted (Appendix II) that almost all the tagged fish were immature and thus unlikely to make a spawning migration for 12 months or so. In this connection it is interesting that one fish was recaptured 1103 days after tagging at a spot only three miles from where it was tagged (Tag No. A3184).

Only four fish were returned after a period of freedom exceeding a year. One of these was the fish mentioned above, which travelled from Leschenault Inlet to Geraldton. The other three were taken only a few miles from the places at which they were tagged.

No definite pattern of movement could be traced within the estuaries. Thus in Leschenault Inlet many of the fish tagged at Collie River were taken just outside the river mouth but others were recaptured both in the upper and lower inlet. No seasonal pattern in the distribution within the inlet was evident.

Some distribution of size-classes along the estuaries was indicated by the results of the experimental hauls. Table 10 indicates for two estuaries the size distribution as found at different points sampled within two days.

Of 2000 mullet tagged in the main Leschenault Inlet, only 14 were over 25 cm. in length. Of 2000 tagged in the Main Peel Inlet none were more than 25 cm. in length. However, large mullet are taken at times in the lower estuaries of the main western river systems, but they do not appear in the commercial catches for more than a few weeks of the year. Indeed over 95 per cent. of the mullet taken are immature (21-26 cm.) (Thomson 1950).

On April 1, 1941, 36 mullet between 31 cm. and 44 cm. were taken in 10 in. of water lying just inside the bar of Peel Inlet, which completely prevented passage to the sea. The mullet seemed to be attracted so strongly by the sea-water percolating through the sand bar that they ignored the approach of human beings and these 36 were caught by hand. They consisted of 25 males and 11 females in full roe. Approximately 5 hours after these fish were taken the sea broke through the bar and the remaining fish of similar size immediately went out to sea.

TABLE 10

DISTRIBUTION OF MULLET ALONG ESTUARIES ACCORDING TO SIZE

Estuary	No. Taken	Size Range (cm.)	Chlorinity	
			Midsummer	Midwinter
Peel Inlet				
Bar Pool	49	10.9-19.7	22.7	11.0
Mandurah Bridge	130	17.0-24.4	22.7	11.0
Willies Lake	23	17.0-39.2	5.1	1.0
Leschenault Inlet				
Preston Bank	84	15.4-22.0	22.6	10.6
Collie R. mouth	68	19.0-24.4	17.9	0.2
The Mere	28	18.0-43.0	17.9	0.2

Attention has already been drawn to the circumstances that no seasonal progression of the mode of the frequency distribution of the commercial catch can be traced in the three main western estuaries (Fig. 2), namely Swan River, Leschenault Inlet, and Peel Inlet. Even allowing for comparatively poor cooperation from the fishermen in returning recaptured tagged fish, there is no indication from the tagging results (Appendix II) of such a heavy fishing intensity that the size-class entering the fishery at 21 cm. (L.C.F.) is immediately depleted and no longer exists effectively in the population. It is suggested that the mullet remain in these lower estuarine waters, which are open to commercial fishing only to a size that happens to be about the legal minimum length, whereupon they move upstream to the upper estuarine waters, which are closed to fishing. This accords with the distribution shown in Table 10, the Mere and Willies Lake being in the upper estuary where commercial fishing is not permitted.

Kesteven (1941, 1942, 1947) has suggested that the young mullet spend their time in the lower, more saline parts of the estuary and that typically they move upstream in the II+ year whilst the older fish penetrate to only slightly saline or quite fresh water. The information gained in the Western Australian survey modifies this picture somewhat. Fish of all ages are found in the brackish and freshwater zones, but Kesteven's description of the behaviour of the older fish has been confirmed. The older fish are not found in the lower estuaries except transiently during migration. The large mullet of the eastern coast spend some weeks passing down the estuaries (Kesteven 1941, 1942, 1947), but in the western estuaries, presumably because of the practically nil tides, the large fish seem to move out to sea as soon as they reach the lower estuaries, except when the mouth of the river is completely barred, as occasionally happens at Peel Inlet or quite usually at Salt R. or Margaret R. on the south-eastern coasts, where large fish are often taken.

V. Comparison with Eastern Australian Stocks

Kesteven (1942) believed there to be no interchange between the mullet stocks of western and eastern Australia. There is no evidence to counter this contention, which is supported by the absence of coastal lakes and rivers across the Great Australian Bight. If these two stocks are indeed unmixed by migration, they have remained amazingly similar in all characteristics (Tables 2, 3; Appendix I).

Growth rate is essentially the same. There are slight differences in the means of the body proportion indices, indicating a slightly smaller head in the western mullet. However, the range of values, in both stocks, is so great (see Appendix I and Kesteven (1942) Table 3A) that the small differences in the grand means is not very significant. The range of K is similar, if one ignores the peculiar readings for a catch of 31 fish taken at Mt. Many Peaks in September 1941. Vertebral, fin ray, and scale counts are not very variable in species of mullet and no differences have been found.

Migration and spawning times are identical. The distribution of the age-groups within the river systems is similar and although Kesteven (1942, 1947) gave the impression that the early age-groups are confined to the lower estuaries, subsequent investigations in the eastern rivers reveal that, as in Western Australia, the young also occur in the upper estuaries and fresh water.

Thus although from their spatial separation there would appear little likelihood of the stocks of the eastern and western coasts mingling, there are, nevertheless, no morphological or physiological grounds for separating them into two races.

There is no parallel on the eastern coast for the persistent accumulation of large mullet at Shark Bay but no similar riverless stretch of coast exists on the eastern side of the continent. It may be that the racial history of the species induces the mullet to seek the area of Shark Bay, which is believed to have been a large estuary in bygone geological ages.

VI. Acknowledgments

The data for the years prior to 1946 were collected under the direction of Dr. G. L. Kesteven. Members of the Department of Fish and Game in Western Australia were always cooperative, especially Mr. A. J. Fraser, Chief of the Department, and four of his officers, Mr. J. Gregory and Mr. A. Melsom, who did much of the measuring work, and Mr. L. Smith and Mr. J. Bramley, who assisted in the tagging work. The tagging operations prior to November 1946 were carried out by Dr. D. L. Serventy of the Division of Fisheries, C.S.I.R.O. Mr. D. J. Rochford, the Divisional Hydrologist, provided the hydrological data. Dr. H. Thompson, Chief of the Division, has always been ready with advice and drew attention to several references.

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APPENDIX I

BODY PROPORTIONS — HEAD LENGTH, TRUNK LENGTH, AND CAUDAL LENGTH AS PERCENTAGE OF TOTAL LENGTH

Sample	Origin	Number	Mean T.L.	Mean $\frac{100\text{H.L.}}{\text{T.L.}}$	Sample Mean —Grand Mean	Sample Range	Mean $\frac{100\text{Tr.L.}}{\text{T.L.}}$	Sample Mean —Grand Mean	Sample Range	Mean $\frac{100\text{C.L.}}{\text{T.L.}}$	Sample Mean —Grand Mean	Sample Range
1.	Augusta	6	30.07	18.13	—1.23	2.4	35.11	1.02	1.80	46.64	1.47	3.20
2.	Swan R.	9	22.80	19.29	—0.07	0.97	34.88	0.79	1.79	45.80	0.63	1.73
3.	Swan R.	24	17.50	19.05	—0.31	3.36	34.33	0.31	5.00	45.11	—0.06	6.00
4.	Swan R.	21	21.90	20.06	0.70	3.10	32.95	—1.14	2.00	46.70	1.53	3.60
5.	Swan R.	7	16.61	20.23	0.87	2.82	34.36	0.27	1.96	45.41	0.24	2.10
6.	Murchison R.	2	44.60	17.93	—1.43	0.34	37.15	3.06	0.68	44.66	0.51	0.28
7.	Murchison R.	2	28.75	20.17	0.81	0.98	34.08	—0.01	0.10	45.72	0.56	0.40
8.	Peel Inlet	4	27.90	18.37	—0.99	1.80	35.64	1.55	1.10	45.94	0.77	3.70
9.	Peel Inlet	30	25.30							44.44	—0.73	6.00
10.	Peel Inlet	57	19.80							44.69	—0.48	3.20
11.	Augusta	11	34.80							45.10	—0.07	6.00
Grand mean W.A.				19.36			34.09			45.17		
Grand mean eastern Australia				18.64			35.36			45.93		

APPENDIX II

NUMBERS TAGGED IN EACH LOCALITY

Locality	Date	Age	No. Tagged	No. Retaken	Percentage Retaken
Swan River	11.iv. 45	I+	43	2	4.6
	28.iii. 46	I+	46	0	0
	9.iv. 46	I+	10	1	10
	10.iv. 46	I+	50	0	0
	11.iv. 46	I+	22	0	0
	29.x. 46	I+	51	0	0
	25.xi. 46	I+	51	0	0
	27.xi. 46	I+	160	0	0
	2.xii. 46	I+	56	0	0
	9.xii. 46	I+	7	0	0
	20.i. 47	I+	3	0	0
	20.v. 47	I+	3	0	0
	13.i. 48	I+	11	0	0
	16.i. 48	I+	10	1	10
	2.i. 49	I+	20	0	0
	3.i. 49	I+	7	0	0
	Total		550	4	0.73
Peel Inlet	10.iv. 45	II+; III+	31	2	6.4
	17.iv. 45	I+	5	0	0
	20.i. 47	I+; II+; III+	23	0	0
	21.i. 47	O+; I+	49	0	0
	8.iv. 47	I+	28	1	3.6
	23.iv. 47	I+	72	5	6.9
	30.vii. 47	II+	119	1	0.9
	24.i. 48	I+	60	1	1.6
	26.i. 48	I+; II+	207	3	1.4
	29.i. 48	I+; II+	346	0	0
	4.ii. 48	I+	62	1	1.6
	5.ii. 48	I+	187	6	3.2
	19.ii. 48	I+; II+	282	1	0.4
	8.iii. 48	I+; II+	109	2	1.8
	31.iii. 48	I+; II+	300	5	1.6
	25.iii. 48	I+; II+	100	1	1.0
	2.v. 48	I+	71	0	0
	Total		2051	30	1.41
Leschenault Inlet	10.i. 46	I+	8	0	0
	18.xi. 46	O+	11	0	0
	19.xi. 46	O+; I+	88	4	4.5
	17.ii. 47	I+	43	2	4.6
	18.ii. 47	I+	142	9	6.3
	19.ii. 47	I+	46	1	2.1
	11.xii. 47	I+; II+	10	0	0
	3.i. 48	II+	51	1	1.9
	19.i. 48	I+; II+	79	4	5
	20.i. 48	I+; II+; III+; IV+	98	2	2
	21.i. 48	I+; II+	133	4	3

APPENDIX II (*Continued*)

Locality	Date	No. Tagged	No. Retaken	Age	Percentage Retaken
	24.ii. 48	I+; II+	177	2	1.1
	25.ii. 48	II+; III+	71	0	0
	3.xi. 48	I+; II+	35	4	11.4
	4.xi. 48	I+; II+; III+	117	3	2.5
	5.xi. 48	I+; II+	43	1	2.3
	25.xi. 48	I+; II+	133	1	0.8
	26.xi. 48	I+; II+	22	0	0
	8.xii. 48	I+; II+	10	0	0
	9.xii. 48	I+	289	0	0.3
	10.xii. 48	I+; II+	15	1	6
	11.xii. 48	I+	123	0	0
	12.xii. 48	I+; II+	157	1	0.6
	13.xi. 48	I+; II+	137	0	0
	25.i. 49	I+; IV+	43	0	0
	27.i. 49	I+	41	1	2.4
	31.i. 50	I+; II+	10	0	0
	1.ii. 50	II+	98	3	3
	Total		2230	45	2.02
Wilson's Inlet	13.ii. 47	I+	2	1	25
	14.ii. 47	I+	4	1	25
	15.ii. 47	I+; II+	65	10	15.4
	8.iv. 48	O+; I+	4	0	0
	Total		75	12	160
Greenough R.	5.vii. 47	O+; I+	2046	5	0.2
Hopetown	14.ii. 46	I+	1	0	0
Moore R.	9.i. 47	I+	10	0	0
Mt. Many Peaks	5.ii. 47	II+; III+	3	0	0
Nannerup	6.ii. 47	I+	7	0	0
Tor Bay	8.ii. 47	O+; II+	8	0	0
Kalgan R.	11.ii. 47	I+	120	0	0
Wonnerup	20.ii. 47	I+	3	0	0
Warriup	24.xi. 48	I+	6	0	0
	Total		7110	96	1.36

APPENDIX III

DETAILS OF TAGGING RETURNS GROUPED IN LOCALITIES AND IN ORDER OF RETURN

Tag No.	Where Tagged	Where Retaken	Date Tagged	Date Retaken	Days Free	Miles Moved	Length Released (cm.)	Length Retaken (cm.)	Growth (cm.)
Leschenault Inlet									
11701	Preston Bank	Upper Inlet	19.xi. 46	20.xi. 46	1	7½	22.0	22.0	0
11683	Preston Bank	Upper Inlet	19.xi. 46	6.i. 47	48	7½	19.4		
11753	Preston Bank	Upper Inlet	19.xi. 46	10.i. 47	52	7½	18.4	19.5	1.1
11727	Preston Bank	Midinlet	19.xi. 46	18.v. 47	180	1	18.6		
A1981	Collie R.	Midinlet	18.ii. 47	23.ii. 47	5	2	21.7	21.7	0
A3541	Collie R.	Collie Bridge	18.ii. 47	7.iii. 47	17	½	22.0	22.0	0
A3568	Collie R.	Midinlet	18.ii. 47	7.iii. 47	17	2	20.5	20.5	0
A3562	Collie R.	Headinlet	18.ii. 47	13.iii. 47	23	6	21.0	21.0	0
A3413	Collie R.	Midinlet	18.ii. 47	12.v. 47	82	1	20.4		
A3407	Collie R.	Midinlet	18.ii. 47	19.v. 47	88	1	23.6		
A3501	Collie R.	Midinlet	18.ii. 47	19.v. 47	88	1	19.7		
A3453	Collie R.	Midinlet	18.ii. 47	28.vii. 47	159	1	21.0		
A3542	Collie R.	Midinlet	18.ii. 47	4.ix. 47	198	1	18.9		
B4715	Collie R.	Collie Bank	3.i. 48	13.i. 48	10	½	22.4		
C29	Collie R.	Kingfisher Pt.	19.i. 48	29.i. 48	10	2	22.8		
C165	Collie R.	Australind	20.i. 48	29.i. 48	9	2	22.5		
C312	Collie R.	Collie Bank	21.i. 48	28.i. 48	7	½	24.0		
C282	Collie R.	Collie Bank	21.i. 48	30.i. 48	9	½	21.5		
A3183	Preston	Collie Bank	17.ii. 47	17.ii. 48	365	1½	21.5	30.5	9.0
C336	Collie R.	Headinlet	21.i. 48	17.ii. 48	28	6	25.2		
C139	Collie R.	Collie Bank	20.i. 48	22.ii. 48	33	½	20.5		
C30	Collie R.	Collie Bank	19.i. 48	22.ii. 48	34	½	21.1		
C315	Collie R.	Collie Bank	21.i. 48	6.iii. 48	46	½	22.7	24.2	1.5
C71	Collie R.	Bunbury	20.i. 48	6.iv. 48	77	3	21.0	24.0	3.0
C39	Collie R.	Australind	19.i. 48	12.iv. 48	84	2	20.7	24.1	3.4
C536	Collie R.	Australind	24.ii. 48	12.iv. 48	48	2	20.4	22.0	1.6
C669	Collie R.	Rathmines	24.ii. 48	15.iv. 48	51	2	22.5	24.6	2.1

APPENDIX III (*Continued*)

Tag No.	Where Tagged	Where Retaken	Date Tagged	Date Retaken	Days Free	Miles Moved	Length Released (cm.)	Length Retaken (cm.)	Growth (cm.)
Leschenault Inlet									
B73	Collie R.	Australind	3.xi. 48	12.v. 48	190	2	25.1		
B427	Collie R.	Midinlet	4.xi. 48	3.xii. 48	29	1½	29.8		
B90	Collie R.	Midinlet	3.xi. 48	10.xii. 48	37	1½	26.8		
B4770	Collie R.	Midinlet	3.xi. 48	10.xii. 48	37	1½	28.5	29.9	1.4
B4795	Collie R.	Bunbury	11.xi. 48	16.xii. 48	42	2	23.0		
C530	Collie R.	Midinlet	24.ii. 48	17.xii. 48	297	2	22.4		
A3842	Rathmines	Kingfisher Pt.	9.xii. 48	23.xii. 48	14	½	18.5	18.5	0
B1900	Kingfisher Pt.	Kingfisher Pt.	12.xii. 48	23.xii. 48	11	0	20.2	20.2	0
B4761	Collie R.	Midinlet	3.iv. 48	5.i. 49	63	2	22.4	24.0	1.6
B36	Hough's Bk.	Midinlet	3.xi. 48	14.i. 49	63	½	25.8	27.8	2.0
B3908	Collie R.	Bunbury	28.xi. 48	25.i. 49	62	2	24.6	27.0	2.4
B242	Rathmines	Australind	11.xii. 48	2.ii. 49	53	3½	17.6	21.4	3.8
B2193	Vittoria B.	Australind	27.i. 49	2.ii. 49	6	3	21.5	21.5	0
A3184	Preston	Australind	17.ii. 47	23.ii. 50	1103	3	20		
B772	Collie R.	Collie Bk.	1.ii. 50	2.iii. 50	30	1½	23.2	25.2	2.0
B784	Collie R.	Collie Bk.	1.ii. 50	2.iii. 50	30	1½	22.6	24.1	1.5
B783	Collie R.	Collie Bk.	1.ii. 50	24.iii. 50	52	1½	24.2	27.0	2.8
A4431	Collie R.	Geraldton	10.xii. 48	9.iv. 40	485	350	18.4	32.4	14.0
Peel Inlet									
11093	Willies L.	Creery Bch.	16.iv. 45	20.iv. 45	4	3	22.8	22.8	0
11108	Willies L.	Creery Bch.	16.iv. 45	3.i. 46	262	3	24.2	27.2	3.0
A626	Mandurah	Harvey R.	23.iv. 47	23.vi. 47	61	12	19.0		
A628	Mandurah	Creery I.	23.iv. 47	3.vii. 47	71	3	19.3		
A935	Mandurah	Main Inlet	23.iv. 47	7.vii. 47	75	1	20.3		
A938	Mandurah	Creery I.	23.iv. 47	28.vii. 47	96	3	19.7		
A606	Mandurah	South Inlet	23.iv. 47	30.vii. 47	98	5	22.7		
A996	Mandurah	Harvey R.	20.vii. 47	27.xi. 47	120	12	25.1		

APPENDIX III (*Continued*)

Tag No.	Where Tagged	Where Retaken	Date Tagged	Date Retaken	Days Free	Miles Moved	Length Released (cm.)	Length Retaken (cm.)	Growth (cm.)
Peel Inlet									
C1028	Mandurah	Main Inlet	24.i. 48	29.i. 48	3	5	19.9	19.9	0
A4288	Mandurah	Long I.	26.i. 48	23.ii. 48	28	1	18.6		
C1455	Mandurah	Long I.	4.ii. 48	7.iii. 48	33	1	19.7		
C1550	Mandurah	Long I.	5.ii. 48	7.iii. 48	32	1	19.6	19.7	0.1
C1604	Mandurah	Long I.	5.ii. 48	7.iii. 48	32	1	20.5		
C1618	Mandurah	Long I.	5.ii. 48	7.iii. 48	32	1	21.5	21.6	0.1
C1662	Mandurah	Long I.	5.ii. 48	7.iii. 48	32	1	20.8	20.9	0.1
C2037	Mandurah	Mandurah	8.iii. 48	23.iii. 48	16	0	22.8	22.8	0
C1984	Mandurah	Mandurah	8.iii. 48	31.iii. 48	24	0	18.1	18.1	0
C2564	Mandurah	Main Inlet	25.iii. 48	14.iv. 48	22	1½	23.0	23.4	0.4
C2392	Mandurah	Main Inlet	21.iii. 48	19.iv. 48	29	1½	22.1	22.8	0.7
A4205	Mandurah	South Inlet	26.i. 48	7.v. 48	102	5	18.9		
C1664	Mandurah	Long I.	5.ii. 48	7.v. 48	92	1	21.5	21.8	0.3
C1830	Mandurah	Outside bar	19.ii. 48	7.v. 48	79	1	19.2	19.6	0.4
C2498	Mandurah	South Inlet	25.iii. 48	7.v. 48	43	5	21.2	21.5	0.3
C2279	Mandurah	Serpentine R.	21.iii. 48	24.v. 48	64	3	19.6		
C2201	Mandurah	Serpentine R.	21.iii. 48	1.vii. 48	101	3	21.5		
C2252	Mandurah	Serpentine R.	21.iii. 48	1.vii. 48	101	3	21.2		
C2420	Mandurah	Long I.	21.iii. 48	1.viii.48	133	1½	20.8	21.7	0.9
C1638	Mandurah	Poverty Pt.	5.ii. 48	5.viii.48	163	4	21.0	24.9	3.9
A4204	Mandurah	Swan R.	26.i. 48	2.xii. 48	310	50	15.4	20.8	5.4
A505	Mandurah	Main Inlet	8.iv. 47	10.xii. 48	620	1½	21.0		
Swan River									
11032	Causeway	Bayswater	11.iv. 45	3.v. 45	21	4	20.9	20.9	0
11046	Causeway	Lucky Bay	11.iv. 45	14.x. 45	186	6	19.3	22.8	3.5
11527	Barkers Br.	Applectoss	9.iv. 46	19.ix. 46	132	18	20.3	20.4	0.1
A4009	Canning R.	Mt. Henry	16.i. 48	29.i. 48	13	2	21.0	21.0	0

APPENDIX III (*Continued*)

Tag No.	Where Tagged	Where Retaken	Date Tagged	Date Retaken	Days Free	Miles Moved	Length Released (cm.)	Length Retaken (cm.)	Growth (cm.)
Greenough R.									
A797	The Bar	¼ Mile from bar	5.vii. 47	3.viii.47	29	¼	13.3		
B370	The Bar	¼ Mile from bar	5.vii. 47	3.viii.47	29	¼	21.5		
B464	The Bar	¼ Mile from bar	5.vii. 47	3.viii.47	29	¼	13.0		
B2066	The Bar	¼ Mile from bar	5.vii. 47	3.viii.47	29	¼	21.8		
B2310	The Bar	¼ Mile from bar	5.vii. 47	3.viii.47	29	¼	14.3		
Wilson's Inlet									
A1448	Denmark R. mouth	State farm	13.ii. 47	15.ii. 47	2	3	21.4	21.4	0
A1458		State farm	14.ii. 47	15.ii. 47	1	3	17.1	17.1	0
A1461	State farm	Main Inlet	15.ii. 47	17.iv. 47	61	6	23.0	23.5	0.5
A1472	Denmark R. mouth	Lower Inlet	15.ii. 47	24.ii. 47	9	8	21.2	21.2	0
A1484	Denmark R. mouth	Lower Inlet	15.ii. 47	24.ii. 47	9	8	22.4	22.4	0
Wilson's Inlet									
A1518	Denmark R. mouth	Lower Inlet	15.ii. 47	24.ii. 47	9	8	21.2		
A1485		Main Inlet	15.ii. 47	28.ii. 47	13	4	20.9	20.9	0
A1508		Lower Inlet	15.ii. 47	26.iii. 47	33	8	22.8		
A1517		Lower Inlet	15.ii. 47	3.v. 47	77	8	22.1		
A1511		Main Inlet	15.ii. 47	29.vii. 47	164	4	24.6	26.8	2.2
A1466		Main Inlet	15.ii. 47	17.vii. 47	183	4	27.5		
A1524		Lower Inlet	15.ii. 47	14.xii. 47	302	8	24.2		

A SURVEY OF THE INLAND FISHERIES OF THE TERRITORY OF NEW GUINEA AND PAPUA

By W. H. SCHUSTER*

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Summary

A survey of two weeks' duration was made of part of the territory of New Guinea and Papua to study the possibility of extending the freshwater and brackish water fisheries. The brackish water region possesses a higher productivity potential than inland waters, owing to the introduction of the normal nutrient components of sea water with the fertile sedimented mud from the rivers, together with organic matter from the rain forests.

Ecologically, and in regard to type of vegetation found, the limited coastal flats, the river deltas, and the extensive mangrove swamps are Indonesian in character. The estuarine region has a fauna rich in density, there being numerous fish species and large populations of prawns, while shrimps and oysters are also plentiful. In the freshwater areas two types of river exist — one shallow, subject to flooding and shifting of sands, and few fish; the second deep, with fertile mud, and fairly productive of fish. The lowland lakes, with fertile colloidal mud, were not examined in detail, but should provide a considerable fishery potential.

There is considerable scope for fish cultural operations, e.g. in constructed ponds.

Before a sound extension of the fisheries can be planned it will be necessary to obtain adequate basic scientific knowledge of the density and composition of the flora and fauna, including the food of the fish stocks, and of the characteristics of the environment. It appears that a fishery more than adequate to supply the protein requirements of the coastal population could therefore be developed, by relatively simple means, in the brackish waters and in the great lowland rivers.

I. INTRODUCTION

At the request of the Department of External Territories, the author visited Papua and New Guinea during the period May 4 to May 21, 1950, to advise the Administration on the extension of the freshwater and brackish water fisheries. Before leaving for New Guinea an attempt was made to gather data concerning the fish fauna and the freshwater fisheries of this area but, with the exception of the taxonomic facts mentioned in handbooks, no information was available either in Australia or in Indonesia. As even the Department of Agriculture, Stock, and Fisheries at Port Moresby possessed no records on the present state of the freshwater and

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brackish water fisheries, the author was entirely dependent on the observation and inquiries made locally during his trip.

At the time of his stay in New Guinea the "Fairwind", a 300-ton motor-vessel of the Royal Australian Navy, was engaged in an examination of the possibilities of marine fisheries, a work carried out under the supervision of the Commonwealth Scientific and Industrial Research Organization. A biologist of the Division of Fisheries, C.S.I.R.O., a technical assistant of the "Fairwind", and an agricultural officer of the D.A.S.F. joined the author on his travels in New Guinea, giving him all possible assistance.

Unlike the situation in areas west of New Guinea, it is a notable fact that the native population of Papua is engaged in sea fishing on a very small scale only. This fact, which was observed during the trips along the north and south coast, was confirmed by Administration and agricultural officers. In some districts fishing with traps is practised and at times people fish also with hand-lines or use simple barrier nets or spears; however, effective gear such as the pajang (seine) or sero (multiple trap) is unknown. Moreover, it should be mentioned that, owing to the lack of roads and quick transportation, local trade in fish and fisheries products is almost negligible. These factors, as well as the rare occurrence of game and the not yet developed stock and poultry breeding, are responsible for the serious shortage of animal proteins in the daily menu of the native people.

The D.A.S.F. officials consider that the fresh and brackish water of New Guinea can provide sufficient fish to overcome the shortage in animal protein. As the D.A.S.F. has so far had no experience in inland fisheries owing to the lack of trained personnel, it was the author's task to estimate the potential of an inland fishery and to make recommendations for initial activities.

II. The Aquatic Flora and Fauna

The territory of Papua and New Guinea, covering an area of 183,000 square miles, includes the eastern part of New Guinea, New Britain, New Ireland, Bougainville, as well as the Admiralty, Trobriand, and D'Entrecasteaux Islands, and the Louisiade Archipelago. As New Guinea is the only territory with rivers, lakes, and estuaries big enough to become of economic importance as fishwaters, the survey was limited to this island.

As it forms part of the Sahul shelf, New Guinea has, where its macroflora is concerned, a clear affinity with the northern part of Australia. Whereas the rain forests in the coastal region are not unlike those in South-East Asia, the typical habitus of the inland part of the country is due to a tropical savannah with a sparse growth of *Eucalyptus* and *Casuarina*. In the limnological field the area shows many peculiarities. According to Weber and de Beaufort's "Handbook of the Fishes of the

Indo-Australian Archipelago" the following species of fish occur in the rivers and lakes of New Guinea:

Isospondyli	Shads	2 species
Siluroidea	Catfishes	29 species
Apodes	Eels	6 species
Solenichthyes	Pipefishes	7 species
Synentognathi	Halfbeaks	8 species
Percesoces	Mullets and threadfins	26 species
Heterosomata	Flatfishes	2 species
Percomorphi	Perches and basses	21 species

In addition to these there are some 40 species of Gobioidea. Many of the species mentioned are euryhaline, i.e. the fishes are able to live in fresh as well as in salt water. Owing to the lack of Cyprinoidea and Labyrinthici, the true freshwater fish fauna of New Guinea is relatively poor in species. Compared with the 500-odd species of fish on the Greater Sunda Islands, a modest 125 species occur in New Guinea.

(*a*) *The Brackish Water Region*

Part of the coast of New Guinea consists of a type of mangrove forest rather similar to that of other countries in the Indo-Pacific area. In some places in a shore strip measuring less than a mile in width, in flat coastal regions, and in the deltas of the big rivers, the mangrove covers an area of many hundreds of square miles. The writer had an opportunity to study mangrove swamps on the South Coast near Yule Island, in the Labu lagoon near Lae, and at the mouth of the Sepik River.

Ecologically there is hardly any difference between a mangrove swamp in Indonesia and one in New Guinea. A grey to brown clay soil with a high content of non-destructible organic matter and an abundance of shell and coral fragments was found. This type of soil appears to be of fine soil particles, which have been colloidally suspended in the water of a river, precipitated after mixing with sea water. Owing to the severe erosion, the water of the rivers in New Guinea carries down the most fertile particles of the soil from the mountains. In the coastal region the sedimented mud is further enriched by the organic matter from the rain forests, and organic plant nutrients are added by the sea-water. Owing to this interaction the soil and the water of the brackish water region possess a higher productivity than either the water of the inland or the offshore region.

It is remarkable that the acid reaction, so often observed in waters of rivers with a long course through rain forests, does not occur in New Guinea. The lowest pH value found in a river there was 7.2.

On the brackish water clay mentioned above a vegetation develops that in many respects resembles the mangrove flora in South-East Asia. In the mangrove swamps studied, not one common plant species was observed that is not also known as a typical component of the mangrove vegetation of Java.

The mud flats on the coast of New Guinea bear a vegetation of *Avicennia marina* (Forsk.) with both the varieties: *A. intermedia* Bakh. and *A. alba* Bakh. Further inland *A. officinalis* L. is also found, mixed with *Rhizophora mucronata* Lam. and *R. apiculata* Bl. (*conjugata*). Occasionally *Rhizophora* spp. took root before *Avicennia*.

In the middle of the mangrove zone the following species of trees were found:

Xylocarpus moluccensis Roem., *X. granatum* Koen., *Bruguiera conjugata* Merr., *B. eriopetala* (Forsk.), *B. caryophyloides* Bl., and *B. parviflora* Men. Also *Sonneratia alba* Sm., *S. acida* L., *Lumnitzera racemosa* Willd., *Aegiceras corniculatum* Blanco, *Ceriops roxburghiana* Arn., and *Excoecaria agalocha* L. were found, with an undergrowth of *Acanthus illicifolius* L., *Acrostichum aureum* L., and *Sesuvium portulacastrum* L. (Plate 1, Fig. 1) (see Becking, den Berger, and Meindersma 1922).

The luxuriant growth of the mangrove, the rich appearance of blue-green algae on the soil shortly after draining, and the high content of plankton in stagnant pools are indications of high fertility. The quality of the mangrove swamps on the south coast of New Guinea is estimated to be equal to that of West Java and the soil in the Sepik delta is possibly even better.

The deltas of the big rivers, the coastal lakes, and the many pools and creeks in the mangrove swamps of New Guinea are populated with a host of fishes of which *Mugil, Thryssa, Arius, Polynemus, Lates, Sillago, Toxotes, Anguilla, Muraenesox,* and the Gobiidae and Eleotridae are the most prominent genera. This estuarine fish fauna shows much similarity to that in the mouths of the big rivers of Borneo and Sumatra, which can be explained by the wide distribution of the euryhaline species. Our own observations, as well as those of Hardenberg in the eastern part of New Guinea, point to a high density of the estuarine fauna.

In addition to fish, the brackish water area does produce a large quantity of crustaceans. Penaeid prawns were found in the mangrove swamps, and freshwater shrimps, probably belonging to the Palaemonidae, appear further inland.

According to information obtained, the abundance of prawns in some areas of New Guinea should be great. The author heard of big quantities of prawns in the Sepik River area, and in all probability most of the brackish waters of New Guinea will prove to be a profitable area for a prawn fishery. Prawns and shrimps can easily become a valuable article of food for the native population as cheap preservation by drying and salting is possible.

Along the coast, the presence of oysters was frequently observed. In many places the stilt roots of *Rhizophora* were completely covered with oysters, which can be easily collected. Not only cockles and mussels, but the oysters too form a part of the daily food of the inhabitants of the coastal villages.

(b) *The Freshwater Area*

(i) *The Rivers.*—For practical purposes the rivers of New Guinea can be divided into two types. One is the "sand river"; here the Markham River can be mentioned as a typical example. Flowing along a wide valley, the river forms a number of branches, which are broad, shallow, and constantly changing in shape, owing to the unceasing shifting of sand on the river bed. The incessant movement of sand, the shallowness, and the occasional floods are the reason why these rivers are poor fish waters.

The second type is the "lowland river", which, owing to its deep bed, the regular flow of water, and the fertile mud, is fairly productive. An example of this type is the Sepik River.

Very little is known about the fish fauna of these waters. Siluroidea of the genera *Copidoglanis* and *Porochilus,* Percesoces of the genera *Melanotaenia* and *Rhombatractus,* as well as many Apodes and Gobioidea are the principal elements of a rather dense fish population. Of the Sepik River it is related by eye-witnesses that each year young eels find their way upstream in great numbers, and big eels migrate back to the sea in other periods of the year. Also, "whitebait", probably a species of the clupeoids, and "bigmouth", a gobioid, are temporarily occurring in the river in large quantities. It is a significant fact that, scientifically, nothing is known of these migrations, which include thousands of tons of fish that are easy to catch.

(ii) *The Lakes.*—The author was only able to visit a single lake, namely Lake Wanam near Lae (Plate 1, Fig. 2). Covering an area of about 10 square miles and situated in a mountainous region 200 feet above sea-level, the lake contains clear water with a pH of 8.3 and plankton on a moderate scale. A scanty, submerged vegetation of *Ceratophyllum,* developed on a bottom layer of coarse calcareous sand and bog with *Nelumbium* and rushes, is present in some bights and creeks. From time to time the lake is visited by natives for the purpose of catching tortoises. As far as could be established during the short visit, Lake Wanam contains only a very limited stock of fish.

Lakes of a totally different type from that mentioned above are found along the Fly and Sepik Rivers and in many places along the coast. The author was only able to observe these lakes from the air. As they are connected with rivers or creeks abounding in fish, and because of a constant addition of fertile, colloidal mud, these lowland lakes offer better facilities for a fish population than the lakes in the hills. In an estimation of the fisheries potential the lowland lakes are a factor that certainly should not be overlooked.

(iii) *The Swamps.*—Along rivers, as well as in natural basins in the hills and on higher ground in New Guinea, there are many freshwater swamps. Some of these bodies of water in the neighbourhood of Port Moresby (Plate 1, Fig. 3) were studied by the writer. With a soil of bog-like consistency, almost completely covered with *Ceratophyllum, Hydrilla, Nelumbium,* and *Nymphea,* these swamps show a remarkably high pH (7.2-7.5) and a high content of zoo- and phyto-plankton. The scanty autochthonous fish fauna is unable to utilize the food production of these waters to full capacity.

(iv) *Conclusions.*—The taxonomic investigation of the flora and fauna of the inland waters of New Guinea is still far from complete. Very little is known of the specific composition of the freshwater fish stock, and biological and ecological data are almost non-existent . There is also a big gap in the knowledge of the composition of the microfauna and flora, which constitute the principal food of the fishes.

It is owing to these circumstances that the scientific basis, which is the fundamental issue in judging the possibilities for fisheries, is still so poor that the expansion of limnological research must be regarded as a prerequisite for further work. So long as nothing is known about the density of the autochthonous fish stock and the quantity of food present in the natural waters, there is only empirical fisheries experience on which to rely. A sound technical extension of fisheries is dependent on the scientific basis mentioned above.

III. The Brackish and the Freshwater Fisheries

(*a*) *Brackish Water Fisheries*

Although the abundance of fish gives the brackish water area of New Guinea the appearance of being an attractive fish water, the native population only capture fish on a small scale. In the course of the investigations the following gear was sporadically found in the villages:

(i) Wide-meshed gill nets made from wartime camouflage nets with floats of light wood, used to fence creeks at outgoing tide.

(ii) Square lift nets stretched between two crossed wooden sticks, used to catch small fish and shrimps in shallow water (Plate 1, Fig. 4; Plate 2, Fig. 4).

(iii) Spears consisting of a bundle of 4 to 10 pieces of wire with sharp points fastened to a wooden shaft, used to spear fish in rivers and along the shore; also occasionally used from boats.

(iv) Traps made from bamboo or rattan in different shapes and sizes, closely resembling the traps used in Siam and Indonesia. Only efficient gear observed in New Guinea. (Plate 2, Figs. 1 and 3.)

(*b*) *Brackish Water Fish Culture*

During his tour of inspection the author tried to check on the possibility and the expediency of the construction of brackish water ponds. He found:

(i) In many places a rich alluvial clay soil suitable for the construction of ponds.

(ii) Extensive sites where the presence of natural channels would warrant the layout of big groups of ponds.

(iii) A tidal movement that, according to information and observation of the water marks, shows an average high water level of about 2 ft. 6 in. above ground level. Therefore, 4 ft. dikes would be adequate to protect the ponds against flooding.

(iv) The occurrence of *Chanos chanos* (Forsk.), the species of fish commonly cultivated in brackish water ponds. Full-grown *Chanos* ("milkfish") were reported by the "Fairwind" from Port Moresby, Port Glasgow, and Salamaua. There was no time left to investigate the occurrence of *Chanos* fry along the coast of Papua and New Guinea.

(*c*) *Freshwater Fisheries*

During his stay in New Guinea the author was able to make a limited number of observations of the fishery in the central part of the island. His opinion in regard to the development of those fisheries is for the greater part based on a general experience in tropical inland fisheries, rather than on research of local details.

In some of the rivers there is extensive fishing; for instance, the fishery in the middle and the lower course of the Sepik is considered to be the most important industrial operation of the native population. Processing of fish and prawns by smoking is known here and the cured products are bartered and traded everywhere along the river. The gear in use is similar to that described in the foregoing chapter. It is probable that similar fishing operations are carried out along other rivers too.

According to information received, fishery by the natives in the mountainous central part of New Guinea is rather restricted, the main reason for this being the comparative dearth of fish in rivers and lakes. The fact that the villages, situated on the top or crests of hills, are usually far away from any possible fish water, may also have a bearing on this. An aversion to fishery or fish consumption was not observed anywhere, the inland fisheries of New Guinea being at the present time simply an industry that—owing to lack of interest—has not yet made any headway.

(*d*) *Fish Culture*

Breeding or rearing of fish or other cultural operations are not established in New Guinea at the present time. The only point that can be mentioned in this connection is an attempt to introduce brown trout in the central mountain area. In 1949, 15,000 young trout were brought by plane from Australia to Nondugl in the Hagen Mountain (Plate 2, Fig. 2), where the fish were partly released in streams and partly in a pond on the Agriculture Station. During a visit to Nondugl there was no evidence of the trout. With a sufficient supply of animal food and a favourable temperature, the water conditions are suitable for trout, but the chance that the streams of the Hagen mountains will become good trout waters is minimized by the many floods during the wet season. The muddy water of the floods is a danger to all types of fish accustomed to clear water. There is no objection on biological or technical grounds, however, to an attempt to introduce trout in the area.

(*e*) *Conclusions*

The population of New Guinea does not derive much benefit from the abundance of fish at the present day. In the deltas, creeks, and lakes of the brackish water area a fishery, adequate to meet the demand for protein by the coastal population and even to produce a surplus, could be developed with relatively simple means. The mouths of the big rivers might even provide a site where an industry of the type of the Bagan Si Api api fishery could be established (Hardenberg 1931).

In view of the presence of large quantities of sea food in the natural waters, the native population cannot be expected to be particularly interested in the construction of brackish water ponds. The construction of a "tambak" would take 3 to 4 years, and considerable skill is necessary to capture fish fry to stock the ponds (Schuster 1949*a*). Moreover, constant supervision of the ponds is essential. On the other hand, the same quantity of fish that a pond would produce in several years can be caught almost directly with less effort in the brackish water area. The construction of ponds along the coast of New Guinea will only be of practical value when the brackish water fisheries can no longer meet the demand for fish.

What has been said in respect of the brackish water fisheries applies equally well to the capture of fish in the lowland rivers. In the stock of fish of the great rivers, New Guinea possesses an important food reserve that has been hardly touched. The extent to which the comparatively small fish stock present in the rivers and lakes in mountainous regions can be increased will need to be assessed by an investigation into the question of food supply. The possibilities for breeding fish will be discussed in the next chapter.

IV. FURTHER EXTENSION OF THE FISHERIES

The present population of Papua and New Guinea is estimated at 1,250,000. Assuming that, on an average, fish consumption would amount to only 25 lb. per head per year, 13,750 metric tons of fish will have to be produced annually to meet the initial demand. A reliable estimation of the present yield of the sea and inland fisheries cannot be given because of the absence of any data whatsoever, but it can be assumed that less than 3,700 tons of fish per year are caught at the present time. Means will therefore have to be found to provide an additional 10,000 tons of fish.

Owing to the limited means of transportation, marketing, and preserving, a large proportion of the required fish will have to be made available on the spot if a quick solution of the problem is to be achieved. This means that the inland fisheries will have a big task to fulfil.

The conditions for the production of freshwater fish in New Guinea are favourable. With an ample rainfall equally distributed over nine months of the year, a relatively fertile soil in the valleys of the inland area, and a rich alluvial clay in the flat parts of the coast, the primary requirements for a good fish production do exist. In arriving at this conclusion the favourable results of the pH investigation and the catches of plankton made in the different types of waters have also been considered.

The good use that can be made of these natural conditions depends on the interest taken by the population and the manner in which the fisheries are propagated by the extension services. The ease with which the population at present acquires its daily food would indicate that only simple and labour-saving methods will be acceptable.

The first step towards an improvement of fish production is an *intensification of the capture of fish* in the brackish water area. There is a plentiful supply of fish and its capture will be no more difficult than it is elsewhere under similar circumstances. Much would be achieved by distributing hooks and lines. For instance, the success achieved by the distribution of fisheries material to the native people in south and east Borneo points in that direction. Here a liberal distribution of gear resulted in the export of dried and salted fish being increased from 3,540 metric tons in 1947 to 12,720 tons in 1949.

Distribution of gear, possibly with the help of or through the intermediary of the agriculture or administration offices, will be the first measure to be taken to increase fish production. When contact with the native population has been established by distribution of hooks and lines, the introduction or sale of lift nets, drift nets, or cast nets, of the types commonly used by the native people of East Asia, can be started. It will be useful, too, to check which kind of trap of the different types in use in New Guinea is the most effective, and the common use of this model will have to be encouraged all round. In promoting simple methods of capture an important task rests with the officers of the extension services. Next to agriculture, fishing is naturally the most important source of food for a population that is only accustomed to money economy in a modest way. In matters of food supply, propaganda for better fishery methods is as important as the introduction of better agricultural systems.

Simultaneously with the intensification of the capture of fish, *supervision of the fish waters* will have to be organized. It is of great importance to collect data relating to the species of fish commonly caught in these waters and the quantities landed. The fish production of some of the waters in New Guinea is likely to be low in comparison with the available food resources. In the lower course of the Sepik River, for instance, there is an abundance of phyto-plankton, which is insufficiently utilized by the stock of fish. At some future date the fish production here can probably be increased by the introduction of plankton-feeding fishes. However, so long as nothing is known regarding the qualitative composition of the available food, no definitive indications can be given.

Generally speaking, it can be stated that the fish fauna of New Guinea, mainly consisting of Gobioidea, Siluroidea, and Apodes, displays a marked deficiency in plankton- and plant-feeders. It is almost certain that at some future date the introduction of species that, under similar circumstances, have been successful in Celebes, will have to be considered. In this connection *Trichogaster pectoralis* (Regan), *Helostoma temmincki* C.V., and *Puntius javanicus* (Blkr.) should be mentioned. Probably *Osteochilus hasselti* C.V. will also have to be considered for introduction into lakes and rivers having clear water. The introduction of new species into an area with an ample stock of autochthonous fish is a drastic measure that can only be effected after an exhaustive investigation by experienced men.

" A second developmental possibility is the *introduction of the culture of freshwater fishes in ponds.* Without doubt freshwater fish can be bred and reared on an economically sound basis in New Guinea as the climatological, hydrological, and topographical conditions, as well as the soil, are suitable for this purpose. The question is, however, whether the native people will be sufficiently interested in this industry under present conditions."

On the coast, where fish, shrimps, prawns, and oysters are easily available, interest in pond construction cannot be expected. In the mountain area, where only a few fish occur in rivers and lakes, and where game has become scarce, conditions are different. It should be quite possible to make the people here fish-minded. Consequently the possibility should be considered of constructing ponds by building dams which, using the natural slope of the land, retain the water in basins on the site.

If sufficient care is devoted to such ponds an annual fish production of 500-1,000 lb. per acre can be expected, and even more under favourable conditions. If freely breeding or naturally regenerating species are chosen a minimum of technical knowledge is needed. No objection can be raised against the introduction of *Cyprinus carpio* L. var. *flavipinnis* (Indian carp) and *Tilapia mossambica* Peters (freshwater perch) as there are no fish of economic importance present that could be crowded out.

To start the culture of the fish mentioned a hatchery is indispensable. The transportation by air of breeders from Indonesia or Malaya to New Guinea is practicable when oxygen cans are used, but the fish would have to be taken to suitable ponds immediately on arrival in New Guinea. A hatchery is likewise necessary for propagation and distribution.

To begin with, ten small ponds will be sufficient: five measuring 33 x 66 ft. and five 66 x 132 ft. respectively, so that the total area of the hatchery will be about one acre. The ponds should be provided with gates to ensure efficient draining. A supply of water to maintain a level of 2-3 ft. is sufficient, but a strong flow of water through the ponds is unnecessary. The hatchery should be constructed on a site with fertile soil, protected against flooding. With a view to subsequent transportation of fish fry, preference should be given to a position with good road and air connection. The author is of the opinion that a suitable site could be found in the neighbourhood of Lae. After the imported fish have propagated in New Guinea a beginning can be made with the construction of ponds in the mountain area. However, fish breeding in the highlands could only be attempted at a later stage.

V. Conclusions

If conditions for the production of fish in natural waters and ponds are favourable, it will be necessary first and foremost to interest the native population in an extension of the fisheries. As long as no expert in inland fisheries has taken up the work in New Guinea, an important part of the preliminary work will have to be done by agricultural officers. These facts have been taken into consideration in drafting the following recommendations. As regards the basic limnological work the following operations should be started:

(i) Recording of the species of fish and prawns occurring in rivers, lakes, and swamps.

(ii) A description of the methods of capture employed in the inland and shore waters of New Guinea and a description of the gear. This work will have to be done mainly by fisheries assistants, capable of judging the effectiveness of the methods and the material in use.

(iii) The collecting of data concerning the intensity of the fisheries in relation to the fish population. Here too the provision of trained personnel is essential. The work can be restricted to important bodies of water and can be conducted along with the investigations referred to under (ii).

(iv) Distribution of gear to the native population.

(v) Distribution of locally made fishing gear and steps to promote the manufacture of such material in areas where it is not known.

(vi) The construction of a hatchery serving to store and to breed imported species of fish and for the observation of economically important autochthonous species.

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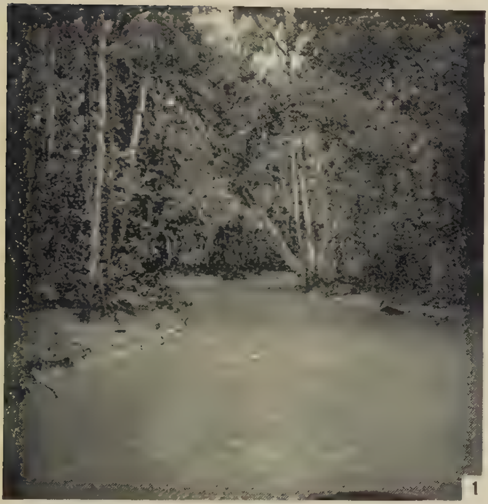
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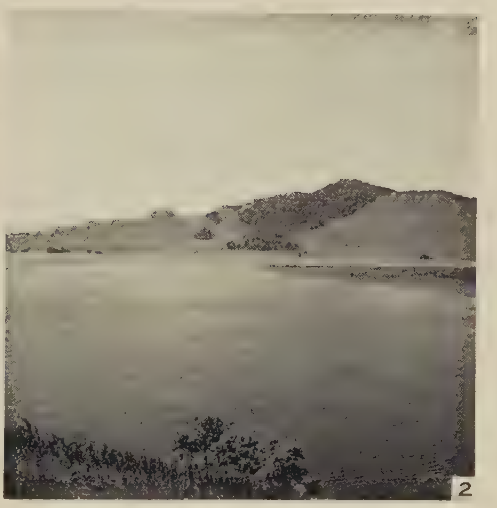
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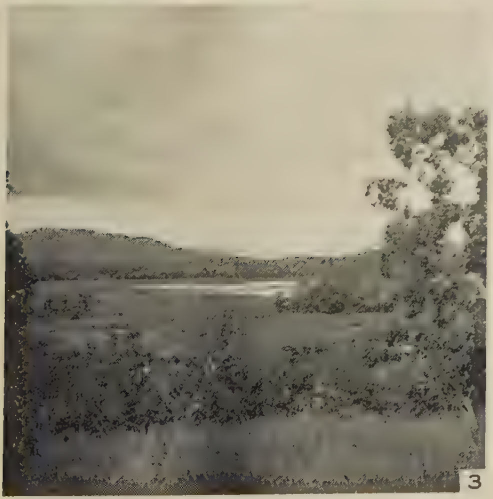
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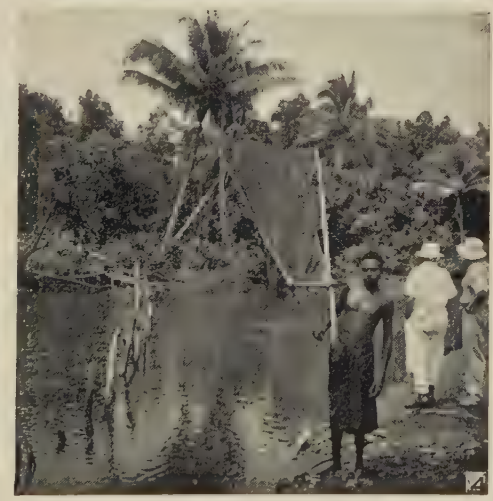
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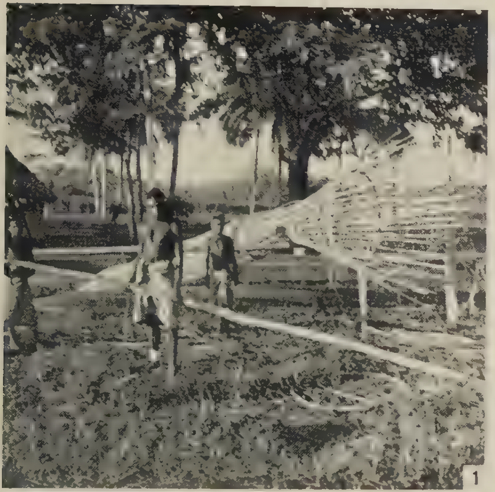
Fig. 1.—Mangrove swamps with *Rhizophora* and *Avicennia* near Yule Island, suited for construction of ponds.

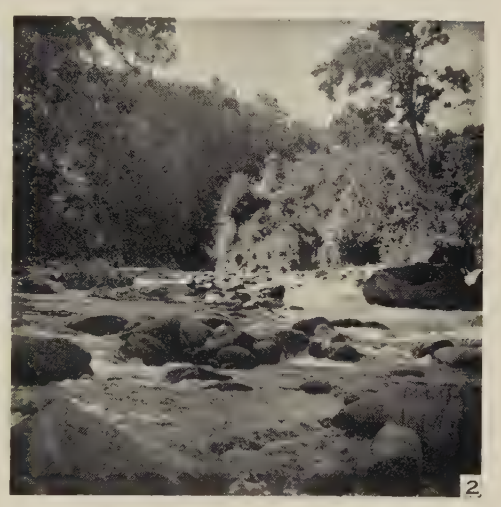
Fig. 2.—Lake Wanam near Lae.

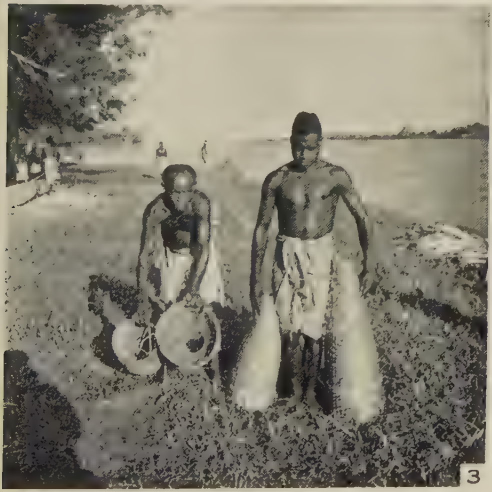
Fig. 3.—Freshwater swamp near Port Moresby with a vegetation of *Nelumbium.*

Fig. 4.—Lift nets.

INLAND FISHERIES OF NEW GUINEA AND PAPUA







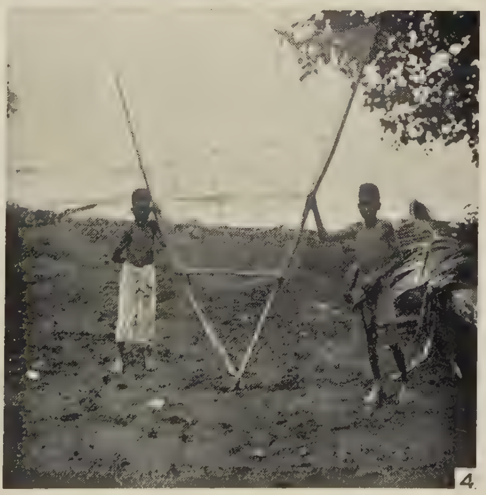


Fig. 1.—Sepik traps.

Fig. 2.—Trout stream near Nondugl.

Fig. 3.—Basket traps locally made on the Sepik River.

Fig. 4.—Scoop nets locally made in a village west of Lae.

CATCH COMPOSITION OF THE SAND CRAB FISHERY IN MORETON BAY

By J. M. Thomson*

(*Manuscript received September* 7, 1950)

Summary

The sand crab industry of Moreton Bay is an expanding fishery. Nets are used in the south of the bay and pots in the north. Three principal grounds are fished within the bay and these yield catches of differing composition. A tendency to sexual schooling is apparent, large males predominating in catches from the southern bay, while the sexes are equally well represented in the north, where the mean size of the males is less. The crabbing grounds vary in productivity, the Scarborough ground producing almost twice as many marketable crabs as the Woody Pt. ground. The percentage of crabs taken that are marketable varied from 55 per cent. in the Cleveland area to 43 per cent. at Scarborough and 34 per cent. at Woody Pt. Female crabs in berry were taken at sizes from 4 to 7.1 in. (carapace width). *Sacculina*-infested crabs were far more numerous on the Woody Pt. grounds than elsewhere. It is recommended that the legal size limits and the restrictions on the take of female crabs be continued, but that *Sacculina*-infested crabs be accepted for market.

I. INTRODUCTION

The regulations upon which the management of the Queensland fisheries is based prescribe that no female crabs may be marketed. The Professional Fishermen's League of Queensland has claimed that female sand crabs with a carapace width greater than 6½ in. are not fertile and therefore crabbers should be permitted to market them. Accordingly, at the request of the Queensland Department of Harbours and Marine, the Division of Fisheries, C.S.I.R.O., undertook a study of the catch composition in commercial operations, especially to ascertain the maximum size at which female crabs with fertile eggs were taken and to determine what proportion of the catch consisted of infertile senile females.

TABLE 1

FISH BOARD DEPOT RECEIVALS OF SAND CRABS, MORETON BAY, 1937-1949

Year	No.	Year	No.
1937	31,835	1944	71,039
1938	59,178	1945	101,074
1939	49,871	1946	99,779
1940	72,969	1947	104,973
1941	86,616	1948	118,921
1942	91,369	1949	223,117
1943	76,252		

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II. Distribution of the Sand Crab

The sand crab of Queensland is *Neptunus* (*Lopha*) *pelagicus,* which is known in other Australian States as the blue swimming crab or blue manna. The species is widespread along the Australian and Indian Ocean coasts and achieves local importance as a fishery product in certain estuaries. It occurs in all the southern Queensland estuaries and probably those to the north, although records are scanty.

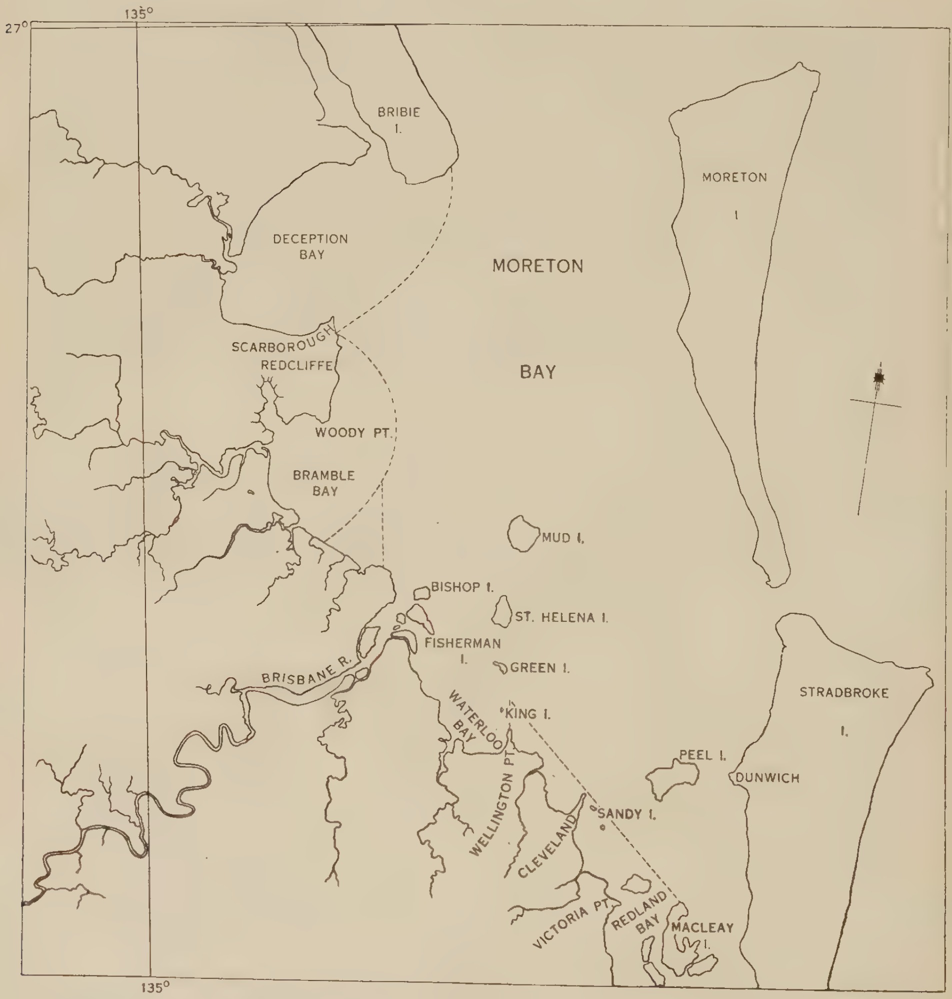

Fig. 1.—Moreton Bay, showing the areas in which crabbing takes place.

III. The Fishery

The major source of the commercial catch in Queensland is Moreton Bay, which supplied 77 and 67 per cent. of the catch in 1948 and 1949 respectively. Accordingly, and as the request concerning the old female crabs came from fishermen in the northern part of Moreton Bay, the study was confined to bay waters. Catch figures are available only from 1937 but indicate a steadily expanding fishery.

Within Moreton Bay there are three principal areas that are fished for sand crabs (Fig. 1). An area to the south and west of Bribie Island is fished by crabbers from Scarborough; crabbers from Woody Pt. fish almost due east of Redcliffe; the third area includes waters adjacent to Wellington Pt., Cleveland, and Redland Bay.

Within Queensland waters it is lawful to use only those kinds of nets prescribed by an Order-in-Council issued by the Governor in Council. Nets for taking crabs are permitted only in certain areas of Moreton Bay (Fig. 1). The total length of the net is not to exceed 200 yards and the mesh of the net is not to be less than 3 in. The prescribed nets are used in the southern part of the Bay, though a mesh of 5 or 6 in. is generally used rather than the permitted minimum of 3 in. The fishermen operating from Scarborough and Woody Pt. at the northern end of the bay do not use nets but use pots, which are actually illegal, but the administrating department has ignored the breach, which does not appear to be harmful. The pots are baited with shark, leather-jacket, or offal fish of various kinds.

TABLE 2

CATCH COMPOSITION OF NEPTUNUS PELAGICUS IN MORETON BAY

	Modal Size	Crabs per Pot	Marketable Crabs per Pot	Male/ Female Ratio	Proportion Marketable	Proportion Males Marketable	Proportion "Hermaphrodites"
Scarborough	6 in.	4.3	1.54	1.8:1	43.2%	68.8%	5.2%
Woody Pt.	6 in.	2.46	0.85	1.3:1	34.0%	49.1%	29.1%
Cleveland	6.1 in.	44*	24*	4.3:1	55.0%	70.0%	4.0%

* Crabs per 200 yards of net.

There does not seem to be any sound basis for restricting the area in which crabs may be taken by nets or pots, nor any reason why fishing by such means should be allowed in Moreton Bay alone of the Queensland estuaries.

The legal minimum size at which a sand crab may be consigned for sale is 6 in. measured across the carapace between the tips of the largest spines.

IV. THE CATCH COMPOSITION

The features of the catch composition are summarized in Table 2.

(a) *Size Frequencies*

The size frequencies of the crabs taken in commercial operations in Moreton Bay are shown in Figure 2. The size curve for each area is practically identical in form, showing the same modes and differing only in the relative numbers of females (Table 2).

It is notable that the modes of the frequency curves fall at 6.1 in., just over the legal minimum size for both male and female crabs. As the latter are not marketed but returned to the water it indicates that the size of the mesh of both pots and nets and the entrances to the pots have been adjusted so that crabs of this size are fished most efficiently.

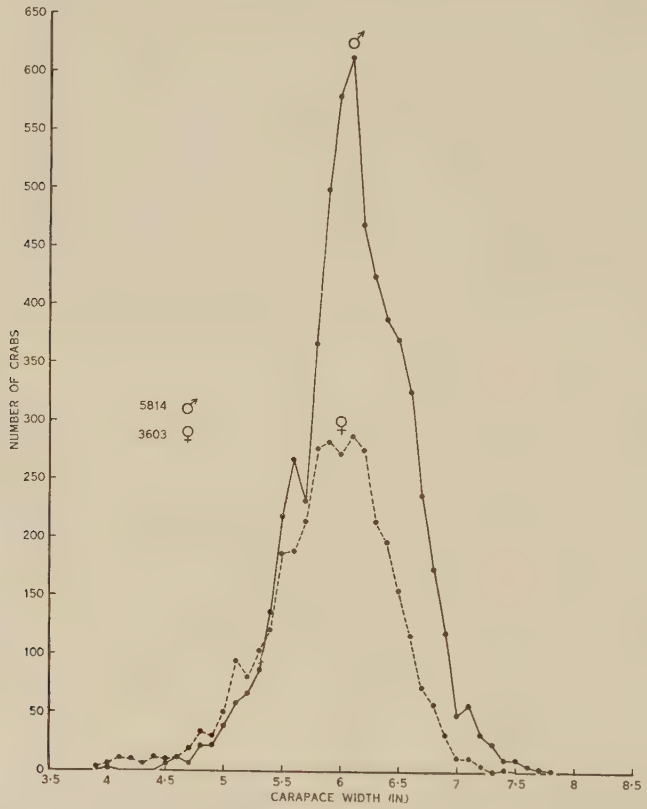

Fig. 2.—Size frequencies of male and female crabs taken in commercial operations.

In the absence of tests with nets and pots of different sizes and apertures it could be argued that this is the size of crab that occurs most abundantly in the commercially fished areas. However, there is no record of the surplus large females being taken elsewhere. The smallest crab recorded from the pots was 4 in., and from the nets 3.4 in.

It is usually accepted that the females mature at the moult when secondary sexual characters become evident, and that males mature at a slightly smaller size (Pearson 1908; Weymouth and MacKay 1936). The secondary sexual characters of the female sand crab become evident at a size of 4 in., so that it can probably be accepted that the present legal minimum of 6 in. permits the crabs to mate at least once before capture.

(*b*) *Catch per Unit of Gear*

The Scarborough crabbing grounds appear to be almost twice as productive as Woody Pt. It is difficult to compare the intensity of catch in the Cleveland area with that of the northern bay, since the fishermen use different methods of capture. But it can be said that in general it would take 11 pots on the Scarborough grounds and 22 on the Woody Pt. grounds to produce the same catch as 200 yards of net in the Cleveland area.

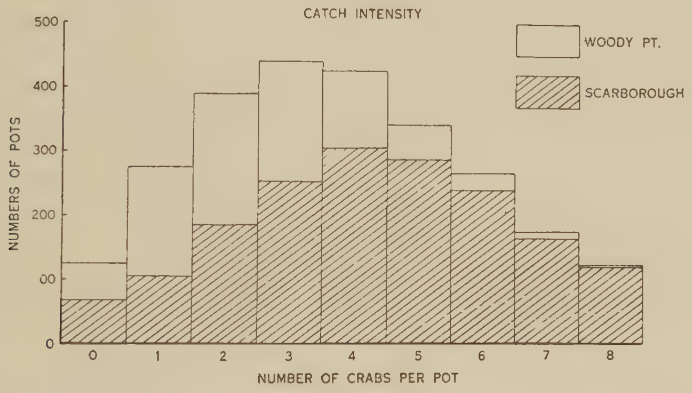

Fig. 3.—Intensity of catch per pot, northern Moreton Bay.

The number of crabs per pot varied from nil to eight (Fig. 3). The number taken per 200 yards of set net varied from nil to 15 dozen. It is a matter of common observation that the catch in the southern part of the bay increases immediately after a northerly wind, and that in the northern part after a southerly. This possibly indicates a general movement in the direction of the prevailing wind if strong; or it could be the result of drift from some central portion of the bay to the periphery where the commercial fishery takes place. But the constancy of the catch composition seems to indicate rather that the crabs that are in waters open to the force of the prevailing wind are stirred off the bottom and thus have more chance of encountering a crab pot or net.

(*c*) *Sex Ratio*

Male crabs are more abundant than female in all three sectors of the bay but their relative abundance is 2½ to 3 times greater in the Cleveland area than in the northern part of the bay. Spencer (1932), investigating the commercial crab (*Cancer magister*) of western North America, found a ratio of 1.28 males to each female.

The greater preponderance of male crabs in the Cleveland area would indicate some swarming or schooling according to sex. Similar tendencies to sexual segregation have been noted previously for *N. pelagicus* by Stead (1898), and segregation is also found in *Cancer magister* (Spencer 1932) and the blue crab (*Callinectes sapidus*) of the Atlantic coast of North America (Fiedler 1930).

(*d*) *Marketable Crabs*

The proportion of the male crabs that were marketable varied according to the source. Of the male crabs taken at Cleveland, 70 per cent. are marketable. This represents 55 per cent. of all crabs taken. At Scarborough 68.8 per cent. of the male crabs taken are marketable, but this amounts to only 43.2 per cent. of all crabs caught in the area. In the Woody Pt. area most of the males are small, only 49 per cent. being marketable, representing 34 per cent. of all the crabs taken.

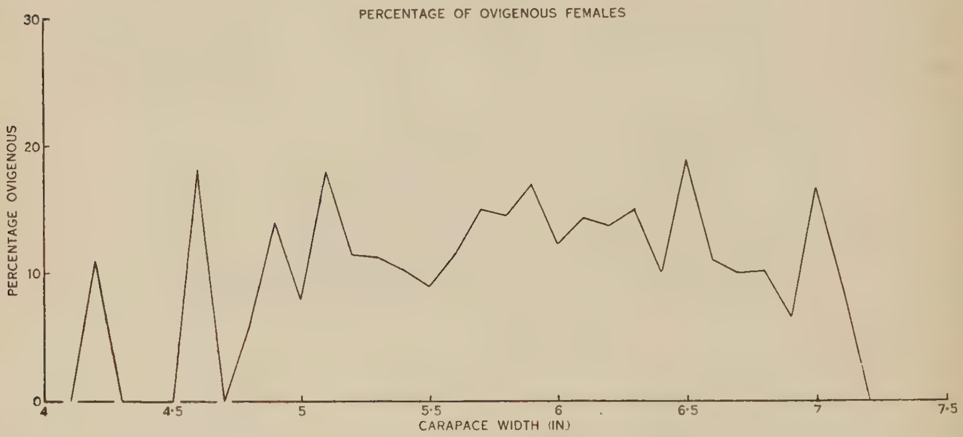

Fig. 4.—Proportion of ovigerous females at each size.

(*e*) *Crabs in "Berry"*

The proportion of female crabs found to be carrying eggs is shown for each size group in Figure 4. The smallest crab bearing eggs was 4.2 in. in carapace width, and the largest 7.1 in. Over the size range 4.2 to 7.1 in., 12.4 per cent. (mean figure) of the females crabs taken were carrying eggs. The fluctuation from the mean is small and is fairly constant over the egg-bearing season (September to April).

It will be seen from Figure 2 that the number of females in each size group drops continually from the peak of 6 in. so that there are few female crabs taken at a size of 7 in. Only a few were taken at a size greater than 7.1 in. and these showed signs of senescence, having the thick elongate claws typical of the male.

(*f*) *"Hermaphrodites"*

There is a class of crabs known to the fishermen as hermaphrodite, which exhibits some male and some female characteristics. These so-called hermaphrodites are actually male crabs infested with the rhizocephalan parasite *Sacculina.*

The effects of the parasitization on the sand crab are much as described for other species by Day (1935). The carapace assumes the relative squatness of the female and the abdomen broadens. Okada and Miyaskita (1935) have described the loss of the male stylets in extreme cases of parasitism in another species of crab. But in all cases of *Neptunus pelagicus* examined the stylets were still present. The female crabs are attacked also but no very obvious change occurs in their external anatomy.

The external portion of the parasite's body is regarded by most fishermen as being the egg-sac of the hermaphrodite crab. According to Day the parasite is present internally for about nine months before the external sac appears. There was no opportunity during the present investigation, which was based on commercial catches, to dissect the crabs to discover the internal parasite. The data on infected crabs (Table 2) refer to those with the parasite showing externally. In the cases investigated by him, Day (1935) found that the external portion of the parasite dropped off during the winter following its appearance, although the internal parasite often survived for a longer period. Presuming Day's findings to apply, the figures for parasitized *N. pelagicus* refer to the crabs infected in a particular year. The degree of infestation varies according to locality (Table 2). Only about 5 per cent. of the crabs in the Cleveland and Scarborough areas were visibly infected by the parasite, but nearly 30 per cent. of those in the Woody Pt. area were infested. Why this should be so is not apparent. As these sterile "hermaphrodites" cannot breed they should be accepted for market or at least removed from the sea where they serve only to increase the stocks of the parasite *Sacculina.*

V. CONCLUSIONS

The present legal minimum size of 6 in. (carapace breadth) seems appropriate. From a subjective estimate it may be said that a crab under $5\frac{3}{4}$ in. is not worth killing for the small amount of flesh contained. It is true that the crabs mature at a lesser size, which is estimated to be about 4 in., when the secondary sexual characteristics become evident (Pearson 1908; Weymouth and MacKay 1936). Female crabs in berry have been noted at 4.2 in. According to Pearson the male (at least in *Cancer pagurus*) matures at a size smaller than the female. It can probably be accepted that the present legal minimum permits the crabs to mate at least once before capture.

Females with fertile eggs have been taken up to a size of 7.1 in. The larger senile female crabs are so few in number (Fig. 4) that little benefit would be derived from amending the regulations to permit them to be marketed.

The so-called "hermaphrodite" crabs are not accepted by the Fish Board depots at present. However, as they are sterile, and so cannot serve to increase the stocks, they should be removed, either for marketing or destruction, rather than being allowed to remain to compete for food or serve as a reservoir of *Sacculina* infection. Crabs infested with *Sacculina* are in most cases quite edible and palatable. About 10,000 more crabs would reach the market if these infected crabs were accepted for sale.

VI. ACKNOWLEDGMENTS

Thanks are due to a number of crabbers for assistance, but particularly to Mr. L. Lohmann and Messrs. H. and L. Kubler from whose boats most of the work in the northern part of the bay was done. The managers of the Fish Board depots at Redcliffe and Cleveland were very helpful. Assistance in the field biometrical work was given by Mr. E. M. Grant. The figures were drawn by Mr. J. Lesslie under supervision of Mr. A. Proctor.

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STOMACH CONTENTS OF NEW ZEALAND INLAND SHAGS

By P. DICKINSON*

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Summary

Twenty-nine stomachs of the large black shag (*Phalacrocorax carbo* (Linn.)) and 61 of the white-throated or little pied shag (*P. brevirostris* (Gould)) from the Rotorua-Taupo area were examined. Techniques used to determine the state of digestion and the identification of otoliths are discussed. Stomach content analyses showed that the food of lake-feeding shags in July consisted almost entirely of fish and freshwater crayfish. Bullies (*Gobiomorphus* sp.) were the most important food fish. Salmonid fish were found in one stomach (*P. carbo*).

I. INTRODUCTION

The only previous work on the food of shags in the Rotorua-Taupo area has been published in a paper by Falla and Stokell (1945). Among locations from which material was examined was Lake Taupo near Waikato River outlet. Fifteen black shags (*Phalacrocorax carbo* (Linn.)) and 40 white-throated or little pied shags (*P. brevirostris* (Gould)) were obtained from this locality, the collector and recorder being Dr. J. Scaife Armstrong. The date of capture is given as "varies between May 1929 and March 1936". The *P. brevirostris* food is commented on as follows: "indicates a strong preference for *Gobiomorphus* followed by *Galaxias* and *Koura* (*Paranephrops*). There are no trout over the whole period of seven years . . ."

The present sample was collected on July 31, 1949, by officers of the Department of Internal Affairs, and by local anglers. The stomachs were preserved in formalin the following morning; thus the time which elapsed between shooting and preservation varied from about 12 to 24 hours. Of the 90 stomachs examined, approximately a third were taken from *P. carbo* (the large black shag) all of which were shot on Lake Taupo. The remaining two-thirds were from the smaller species, *P. brevirostris*, which were shot in about equal numbers on Lake Taupo and Lake Rotorua. Details of locations are given in Appendix I.

II. IDENTIFICATION TECHNIQUE

It was realized that, ideally, both numerical and volumetric analyses should be made. In this report, however, it is not intended to analyse and discuss the contents volumetrically, but the detailed information necessary for this (size range of each species in each stomach) has been recorded and would be made available to other interested workers. Appendices II and III are summaries of these details.

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(*a*) *Bones*

As an aid to identification, the bones of a partially digested carp (*Carassius* sp.) were disarticulated and mounted. Also, a specimen was cleared and stained. However, in some stomachs bones were so numerous that identification of the number of fish and the species, while theoretically possible, would have involved so much time that it was not proceeded with.

(*b*) *Otoliths*

More success attended the identification of otoliths (see Fig. 1). For comparative purposes otoliths were dissected from fish indigenous to the area (*Retropinna* sp., *Gobiomorphus* sp., *Carassius* sp., and *Salmo irideus* (Ayres)). Lack of a suitably sized indigenous fish of the family Galaxiidae necessitated the dissection of otoliths from *Galaxias attenuatus* (Jenyns). From the drawings two significant points are apparent:

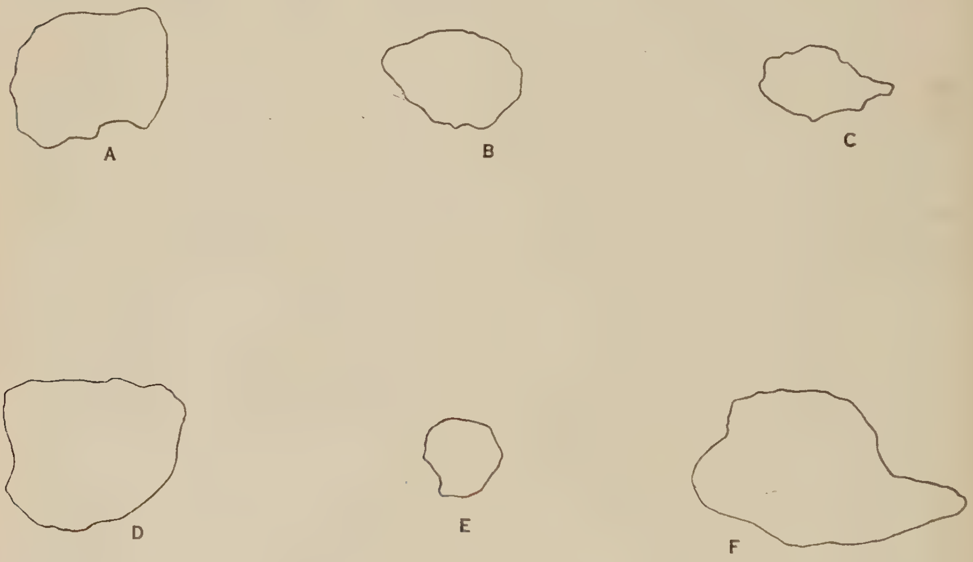

Fig. 1.—Otoliths (all x 4). *A*, *Carassius* sp. (so-called carp), length 9.5 cm. *B*, *Galaxias attenuatus* (whitebait), length 9.5 cm. *C*, *Salmo irideus* (rainbow trout), length 7 cm. *D*, *Gobiomorphus* sp. (bully), length 8 cm. *E*, *Retropinna* sp. (smelt), length 7 cm. *F*, *Salmo irideus* (rainbow trout), length 23 cm.

(i) *Shape.*—Three quite distinctive groups appear: (1) *Carassius* sp. and *Gobiomorphus* sp.; (2) *Retropinna* sp. and *Galaxias attenuatus;* (3) *Salmo irideus.* Except with very worn otoliths, it is unlikely that these groups could be confused.

(ii) *Size.*—In fish of like size, otoliths from *Galaxias attenuatus, Retropinna* sp., and *Salmo irideus* have approximately the same area. Otoliths from *Gobiomorphus,* however, are about eight times as large. *Carassius* otoliths are slightly smaller than those taken from *Gobiomorphus.*

In addition, the otoliths from *Retropinna* and *Galaxias attenuatus* are very fragile, the latter particularly so. It is very unlikely that otoliths from these two fish would persist in a shag stomach longer than the fish themselves.

Taking all the above factors into account the otoliths found in the stomachs were beyond doubt either from *Carassius* or *Gobiomorphus,* and as shown later, it would seem reasonable to assume that they originated in the latter fish.

(*c*) *Digestion*

The origin of the smaller invertebrate forms found in shag stomachs has been mentioned. The evidence produced here on this point is still not conclusive, but further relevant facts are recorded. The state of digestion (and thus the possibility of these organisms having come from the gut of fish taken by the shag) is an important issue, and an attempt has been made to determine the degree of digestion in each stomach. In judging the degree of digestion an arbitrary point was chosen midway down the stomach and the contents at such points were placed into one of four groups (Table 1).

TABLE 1

DEGREE OF DIGESTION OF STOMACH CONTENTS

Index No.	Fish	Freshwater Crayfish	Shellfish
1	Head and belly complete	External skeleton articulated	Flesh present in shell
2	Flesh on head and belly digested (pigmentation partly gone)		Flesh gone, shell hard
3	Head (including bones) digested, skin digested, flesh partially gone	External skeleton disarticulated but still in position, flesh partially digested	
4	Flesh digested, bones only remaining	Remains only (parts of skeleton, mouth-parts, etc.)	Shell crumbling

The groups were first determined for fish, where digestion proceeded in the order shown. It was then relatively simple to place freshwater crayfish and shellfish (where they occurred in the same stomach with fish) in their correct positions on the scale.

III. STOMACH CONTENTS

(*a*) P. carbo

(i) *Fish.*—Two of the 29 stomachs examined were empty. Of the remaining 27 stomachs, 17 contained fish or remains of fish. Disregarding unidentified fish (nine occurrences) and otoliths (eight occurrences), it was found *Gobiomorphus* sp. occurred in five stomachs (4.2 per stomach), *Carassius* sp. occurred in two (2.5 per stomach), and salmonid fish (almost certainly trout) in one.

(ii) *Freshwater Crayfish* (Paranephrops *sp.*).—Of the 10 stomachs that did not contain fish, 4 contained freshwater crayfish (2.5 per stomach) and one the remains of freshwater crayfish.

(iii) *Nematodes.*—Three of the remaining five stomachs contained large numbers of nematodes (340 per stomach). These were *free* in the stomach and no food was present.

(iv) *Mollusca.*—Digestion in the last two stomachs was very far advanced (4+) and contained, in one a single *Limnaea* shell and in the other 20 shells of *Potamopyrgus.*

Shells of *Potamopyrgus* were found in nine stomachs (34 per stomach) and in all cases except the instance quoted above, fish or fish remains (including otoliths) were found with them. In many stomachs with a digestive index of 2, fish were observed with their stomach contents exposed. These fish stomach contents comprised mainly the highly resistant shells of *Potamopyrgus.*

TABLE 2
P. CARBO (29 STOMACHS, 2 EMPTY)

	Gobiomorphus	Otoliths (probably *Gobiomorphus*)	*Carassius*	*Salmo*	Unidentified Fish	*Potamopyrgus*	*Paranephrops*
No. of stomachs	5	8	2	1	9	9	7
No. per stomach	4.2	29	2.5	2	?	34	2.5
Greatest No. found in any stomach	6	78	4	2	?	80	5

(v) *Otoliths.*—Otoliths occurred in eight stomachs (29 per stomach). In five of these *Gobiomorphus* sp. or fish remains were also found. In the other three, digestion was advanced and no fish or fish remains other than otoliths were present.

Much of the above information is summarized in Table 2, which has been prepared from data given in Appendix II.

(*b*) P. brevirostris

(i) *Fish.*—Five of the 61 stomachs were empty. Thirty-four contained fish or fish remains. Disregarding unidentified fish (12 occurrences) and otoliths (25 occurrences), it was found that 23 stomachs contained *Gobiomorphus* sp. (12 per stomach) and 4 contained *Carassius* sp. (1.5 per stomach). No trout were found in any of the stomachs.

(ii) *Freshwater Crayfish.*—Of the remaining 25 that did not contain fish, 22 contained freshwater crayfish (7 per stomach) and two the remains of crayfish. In four instances crayfish (excluding remains) were found in the same stomachs with *Gobiomorphus* sp.

(iii) *Mollusca.*—One stomach did not contain either fish or crayfish. This contained a single *Potamopyrgus* shell and a number of pieces of pumice. *Potamopyrgus* shells were found in 25 stomachs (47 per stomach) and in all cases except the one mentioned above were found associated with fish or fish remains. Remarks on the origin of these snails in the *P. carbo* stomachs apply equally here.

(iv) *Otoliths.*—From *Gobiomorphus* sp. (or *Carassius* sp.) otoliths occurred in 25 stomachs (approximately 100 per stomach). It should be noted that in all except two these occurrences were associated with occurrences of *Gobiomorphus* sp. or fish remains. Otoliths were not found in the same stomachs with *Carassius* sp.

TABLE 3

P. BREVIROSTRIS (61 STOMACHS, 5 EMPTY)

	Gobiomorphus	Otoliths	*Carassius*	*Salmo*	Unidentified Fish	*Potamopyrgus*	*Paranephrops*
No. of stomachs	23	25	4	Nil	12	25	36
No. per stomach	12.2	99.6	1.5	Nil	?	47.2	5.9
Greatest No. found in any stomach	34	382	3	Nil	?	179	12

Table 3 is a summary of information taken from Appendix III. It will be noticed that it is not consistent with data above. This is because the table refers to the total number of occurrences of food animals while the above discussion eliminates food animals in order of importance.

IV. DISCUSSION

(*a*) *Fish and Freshwater Crayfish*

If it is true that *Potamopyrgus* (and other small invertebrate forms) originated from fish taken by the shags, and if two occurrences of frogs are excluded, then the food of these lake-dwelling shags in July consists ntirely of fish or freshwater crayfish. *Gobiomorphus* sp. is the most mportant food fish. *Carassius* sp., *Retropinna* sp., and salmonid fish (in ne instance) were also identified.

Freshwater crayfish are taken in large quantities, particularly in Lake Rotorua and Lake Rotoiti. Here, for every stomach containing *Gobiomorphus* sp. there were more than two containing crayfish. It appears also that it is not usual for shags to engage in mixed feeding—i.e. they feed entirely on crayfish for a period or on *Gobiomorphus* sp. Where the two are found in the same stomach they are separate and not mixed. It would seem that the shag had either changed from one food to the other in the one locality or changed feeding grounds. To gain further knowledge on this point it is essential to have data on the food available in the locality and also to know how long the bird had been feeding there before it is shot.

(*b*) *Mollusca* (Potamopyrgus)

From a study of the occurrences of *Potamopyrgus* and the digestive indices it can be seen that, wherever *Potamopyrgus* was found, digestion had advanced sufficiently to expose the stomach contents of any fish present. In fact a number of fish were observed with the stomach contents fully exposed and with a number of *Potamopyrgus* showing and ready to drop into the cavity of the shag's stomach. It is unfortunate that, owing to the rapid digestion of shags and also the possibility of post-mortem digestion, there were not more instances of freshly taken fish from which escape of the stomach contents would not have been possible. It is desirable that stomachs from these birds should be preserved as soon after shooting as practicable.

(*c*) *Otoliths*

It was shown earlier that the otoliths found in the stomachs were either from *Gobiomorphus* sp. or *Carassius* sp. The occurrence of otoliths in the same stomachs as *Gobiomorphus* sp. and their absence from stomachs containing *Carassius* sp. strongly suggest their originating in the former fish.

In some cases the number of otoliths found is fairly high; the highest recorded being 382. It is not thought that they have accumulated over a long period. When these otoliths are converted into live weight of fish it is not unreasonable to assume that the otoliths came from fish consumed on the same day. We may for instance take 382 otoliths as an example. This is equivalent to 191 fish. The mean length of *Gobiomorphus* sp. taken from the stomachs examined was approximately 5 cm. The wet weight of a fish of this size and species is 1.2 g. Therefore 191 *Gobiomorphus* sp. will weigh 229.2 g. or a little over half a pound. It is difficult to assess the weight of food taken by a shag under natural conditions. This may of course vary with a number of factors, such as age and species. From estimates made here and overseas from experiments with birds in captivity (Serventy 1938; Williams 1945) a reasonable average figure would be ¾-1 lb.

(*d*) *Nematodes*

Apart from *Eustrongylides ignotus* encysted in the stomach wall, large numbers of nematodes were found free in three of the *P. carbo* stomachs. It seems quite certain, in view of the site of these worms, that they are *Contracaecum spiculigerum*. This is a very common parasite of shags and cormorants and is found throughout the world.

(*e*) *General*

It should be realized that the evidence presented in this paper is but a contribution to the problem of the food of inland shags and should be interpreted in the light of two limitations. These are limitations of place and time. The samples, while adequate numerically, were all taken on the same day (in July) and from the same type of water (lakes). Previous works of this nature with samples collected from other types of environment and at other seasons have shown markedly different results. There is also a lack of adequate knowledge of the aquatic life at the feeding grounds and the behaviour of these birds on the grounds so that correlation of this aspect with the stomach contents is not possible.

V. ACKNOWLEDGMENTS

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APPENDIX I

NUMBERS OF SHAGS SHOT AND LOCATION

Phalacrocorax carbo (Large Black Shag)		*Phalacrocorax brevirostris* (White-throated or Little Pied Shag)	
Place	No. Shot	Place	No. Shot
Lake Taupo		Lake Taupo	
Delta	1	Waihi Bay	2
Stump Bay	1	Delta	7
Motutere	3	Stump Bay	1
Motutaiko Island	3	Motutere	2
Whitecliffs	7	Whitecliffs	5
Waitahanui	2	Acacia Bay	6
Dangatiss Pt. ?	4	Jerusalem Bay	3
House Boat	2	Whangamata	1
Acacia Bay	4		27
Jerusalem Bay	1	Lake Rotorua	
Whangamata	1	Unspecified	22
Total	29	Mokoia Island	9
			31
		Lake Rotoiti	
		Unspecified	3
		Total	61

APPENDIX II

STOMACH CONTENTS OF P. CARBO

Locality		*Gobiomorphus*	Otoliths	*Carassius*	*Retropinna*	*Salmo*	Unidentified Fish	*Potamopyrgus*	*Limnaea*	*Paranephrops*	*Olinga*	Ephemeridae	Nematoda	Stones
Lake Taupo	No. of stomachs	5	8	2	1	1	9	9	1	7	1	1	10	11
	Av. No. in each stomach	4	29	2.5	143*	2	—	34	1	1.4	26	?	111	18
	Size range (cm.)	3–13		6–14	3.5	†	—	0.1–0.6	1.9	7.5–10.5	0.5–0.6	?	0.5–5	0.1–2

* Larval fish.

† Age 2 years.

APPENDIX III

STOMACH CONTENTS OF P. BREVIROSTRIS

Locality		Frog	*Gobiomorphus*	Otoliths	*Carassius*	Unidentified Fish	*Potamopyrgus*	*Corneocyclas*	*Limnaea*	*Paranephrops*	Odonata	Chironomid	Nematoda	Stones
Lake Taupo	No. of stomachs	2	11	16	4	10	15	—	2	7	2	1	12	16
	Av. No. in each stomach	1	6.5	49	1.5	—	32	—	1	?	1	1	9	24.5
	Size range (cm.)	5	2–9	—	3–18	—	0.1–0.6	—	0.6–0.8	?	2–?	1	0.5–5	.2–4
Lake Rotorua	No. of stomachs	—	11	8	—	2	9	3	—	26	—	—	5	7
	Av. No. in each stomach	—	15.7	177	—	—	75	3.3	—	6	—	—	3	10
	Size range (cm.)	—	2–8	—	—	—	0.05–0.5	0.1–0.3	—	3–10	—	—	1–5	0.3–1
Lake Rotoiti	No. of stomachs	—	1	1	—	—	1	—	—	3	—	—	1	—
	Av. No. in each stomach	—	26	287	—	—	6	—	—	4.3	—	—	1	—
	Size range (cm.)	—	2.5–5	—	—	—	0.1–0.3	—	—	4.5–8	—	—	4	—

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